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From gametogenesis to spawning: How climate-driven warming affects teleost reproductive biology

Maud Alix[1] | Olav S. Kjesbu[1] | Kelli C. Anderson[2]

[1]Institute of Marine Research, Bergen, Norway
[2]Institute for Marine and Antarctic Studies, University of Tasmania Newnham Campus, Newnham, Tasmania, Australia

Correspondence
Maud Alix, Institute of Marine Research, PO Box 1870 Nordnes, No-5817 Bergen, Norway.
Email: maud.alix@hi.no

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Abstract

Ambient temperature modulates reproductive processes, especially in poikilotherms such as teleosts. Consequently, global warming is expected to impact the reproductive function of fish, which has implications for wild population dynamics, fisheries and aquaculture. In this extensive review spanning tropical and cold-water environments, we examine the impact of higher-than-optimal temperatures on teleost reproductive development and physiology across reproductive stages, species, generations and sexes. In doing so, we demonstrate that warmer-than-optimal temperatures can affect every stage of reproductive development from puberty through to the act of spawning, and these responses are mediated by age at spawning and are associated with changes in physiology at multiple levels of the brain–pituitary–gonad axis. Response to temperature is often species-specific and changes with environmental history/transgenerational conditioning, and the amplitude, timing and duration of thermal exposure within a generation. Thermally driven changes to physiology, gamete development and maturation typically culminate in poor sperm and oocyte quality, and/or advancement/delay/inhibition of ovulation/spermiation and spawning. Although the field of teleost reproduction and temperature is advanced in many respects, we identify areas where research is lacking, especially for males and egg quality from "omics" perspectives. Climate-driven warming will continue to disturb teleost reproductive performance and therefore guide future research, especially in the emerging areas of transgenerational acclimation and epigenetic studies, which will help to understand and project climate change impacts on wild populations and could also have implications for aquaculture.

KEYWORDS
climate change, fecundity, fish, gamete, physiology, temperature

1 | INTRODUCTION

The impact of global warming on teleost reproduction has been reviewed several times over the last couple of decades (Grazer & Martin, 2012; Miranda *et al*., 2013; Pankhurst & King, 2010; Pankhurst & Munday, 2011; Servili *et al*., 2020; Van Der Kraak & Pankhurst, 1997). However, due to the steadily increasing amount of published studies on this topic, rapid advances in relevant methodology (*e.g*., within molecular biology) as well as a general growing public concern about future fish sustainability, a thorough update to build on previous

works is needed. Further to this, it is particularly important to develop this research field as the latest projections from the Intergovernmental Panel on Climate Change were revised upward. Indeed, near-term projections for the global mean sea surface temperature (SST) are +0.64°C and 0.95°C, while at the end of century +0.73°C and 2.58°C are expected for the optimistic (RCP2.6, RCP: Representative Concentration Pathways) and pessimistic ("business-as-usual") greenhouse gas scenarios (RCP8.5), respectively (Pörtner *et al*., 2019). Although on average the earth is getting warmer, extreme values are projected to specifically appear in riverine systems and in Arctic (named Arctic amplification) and Sub-Arctic marine regions [already +1.5°C between 1985 and 2012 in the Barents Sea (Kjesbu *et al*., 2014)] but also result in the increase of extreme event frequency, for example marine heatwaves (Boeke & Taylor, 2018; Pörtner *et al*., 2019).

As most teleosts are poikilotherms, ambient temperature directly impacts metabolic rate, reproductive performance (Vagner *et al*., 2019; Wang *et al*., 2010), body growth, natural mortality and recruitment success (so-called "vital parameters" in population dynamics), and thereby ultimately population (stock) productivity (Kjesbu *et al*., 2014). Depending on the species and life stages, fish sensitivity to thermal fluctuations varies due to their window of thermal tolerance (Pörtner & Farrell, 2008; Dahlke *et al*., 2020). For instance, most sensitive stages to thermal stress, spawning and early life correspond to the narrowest thermal windows. Moreover, spawning temperature is often related to the thermal preferendum of embryos (Pörtner & Peck, 2010). Therefore, investigations on fish reproduction are crucial in the context of global warming, particularly since the reproductive capacity and plasticity of individuals contributes to processes such as adaptation, speciation and eventually extinction in populations subject to climate change (Grazer & Martin, 2012).

In most fish species, the reproductive cycle is mainly dependent on the seasonal rhythm of external factors and therefore appears at regular intervals, for example annually achieving synchronization (Takemura *et al*., 2004; Wang *et al*., 2010). In temperate teleosts, the main environmental driver (*i.e*., determining factors of reproduction) controlling reproductive events but also life history in more general terms is the photoperiod (proximate cue) (Sundby *et al*., 2016), whereas temperature is considered a secondary cue (ultimate factor) (Migaud *et al*., 2010; Wang *et al*., 2010). In more applied terminology photoperiod may be labelled as a "trigger" and temperature as a "regulator" (Kjesbu *et al*., 2010). This because temperature is seldom, formally speaking, a cue as such, although exceptions exist in the teleosts literature, such as initiation of spawning following an abrupt change in temperature. In tropical and equatorial zones, those two factors undergo much less year-round (seasonal) fluctuations. Therefore, in these waters environmental regional modifications drive synchronization of reproductive events, for example rainfall (Denusta *et al*., 2019; Karnatak *et al*., 2018), tides or lunar cycle (for review see Takemura *et al*., 2004; Shima *et al*., 2020), rather than, for example, markedly changing seasonal day lengths as seen at high latitudes (Sundby *et al*., 2016). Moreover, stimuli responsible for activation of the brain–pituitary–gonad (BPG) axis controlling reproductive events may come in various forms, such as genetic, metabolic or environmental signals (Liu *et al*., 2017; Roa *et al*., 2008). In addition to determining factors, modulating factors help in fine-tuning of reproductive progress and quality (Wang *et al*., 2010), such as temperature in some temperate and tropical species (Pankhurst & King, 2010; Takemura *et al*., 2004). This outline should not be taken as an indication that high-latitude species are more at risk under climate change than tropical species. It is rather the opposite, as tropical species are already closer to or at their thermal maximum (*i.e*., narrow thermal windows, but may quickly acclimate) (Donelson *et al*., 2012) whereas, for example, cold-water temperate species typically are on the "ascending limb" of the expected physiological response, forming a dome-shaped curve (Pörtner & Farrell, 2008), and thereby might benefit reproductively by even higher temperatures until the optimum is reached (Kjesbu *et al*., 2010, 2014). Indeed, some species, such as the bluefish (*Pomatomus saltatrix* (Linnaeus 1766)) and Atlantic cod (*Gadus morhua* L.) in the Barents Sea, seem to benefit from the water warming (*e.g*., expansion of distribution, increase in fish condition) (Kjesbu *et al*., 2014; Villegas-Hernández *et al*., 2015).

Among the reproductive processes influenced by temperature [*e.g*., sex determination (reviewed by Geffroy & Wedekind, 2020), early puberty], gametogenesis is particularly interesting as during this process gametes are produced and the final stages of oocyte maturation seem to be highly temperature sensitive (Bobe, 2015; Tveiten *et al*., 2001; Zucchetta *et al*., 2012). Gamete quality is a primary determinate of developmental success in the next generation due to the combined ability of sperm and egg to produce viable offspring (Bobe & Labbé, 2010). Therefore, the comprehension of warming impacts on gametogenesis and their consequences on gamete quality is of great importance for aquaculture as well as reproductive ecology. However, while reproductive performance is a key attribute, it should be realized that populations might do poorly under climate change for other reasons, such as poleward displacement of important predators (Fossheim *et al*., 2015), difficulties associated with long generation cycles (reduced possibility of adaptation), ecological specialization or overexploitation (Dulvy *et al*., 2003; Hillebrand *et al*., 2018), and temperature-driven changes in reproductive timing and capacity will interact with these variables.

The present review aims to examine current progress in the understanding of warming effects on fish reproduction from tropical to temperate environments and to highlight future research priorities in this field. For that purpose, we will focus on adult teleost gamete development, maturation, release (spawning) and quality, mainly in females but also in males, including endocrine factors controlling these processes and transgenerational considerations. However, this synopsis will be uneven across taxa and reproductive stages due to a skewed number of published studies. We aim to investigate temperature-driven changes in reproductive function and the underpinning mechanisms at different scales (molecular, cellular and individual), which altogether are facets in the large, complex picture of aquaculture and fisheries sustainability.

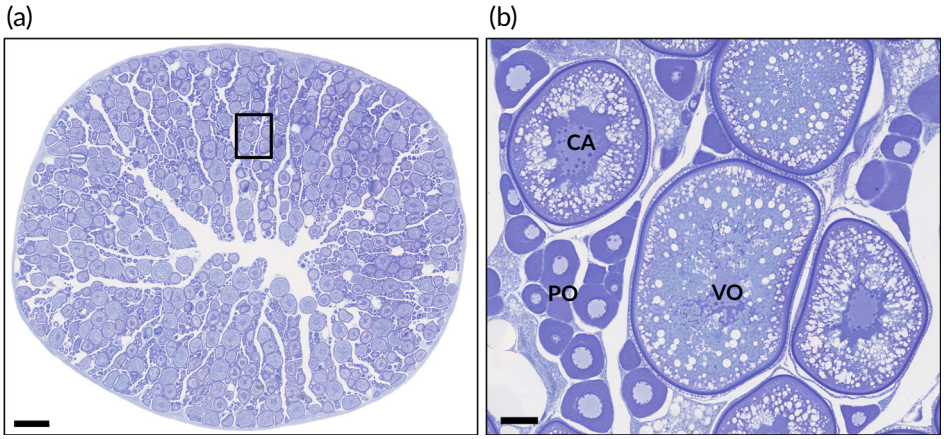

FIGURE 1 (a) Transverse section of mackerel ovary embedded in Technovit, stained with toluidine blue and digitalized using a slide scanner (NanoZoomer S60, Hamamatsu Photonics, Boston, MA, USA). Scale bar: 1 mm. Black square in (a) is magnified in (b). (b) CA, cortical alveolus; PO, primary oocyte; VO, vitellogenic oocyte. Scale bar: 100 mm

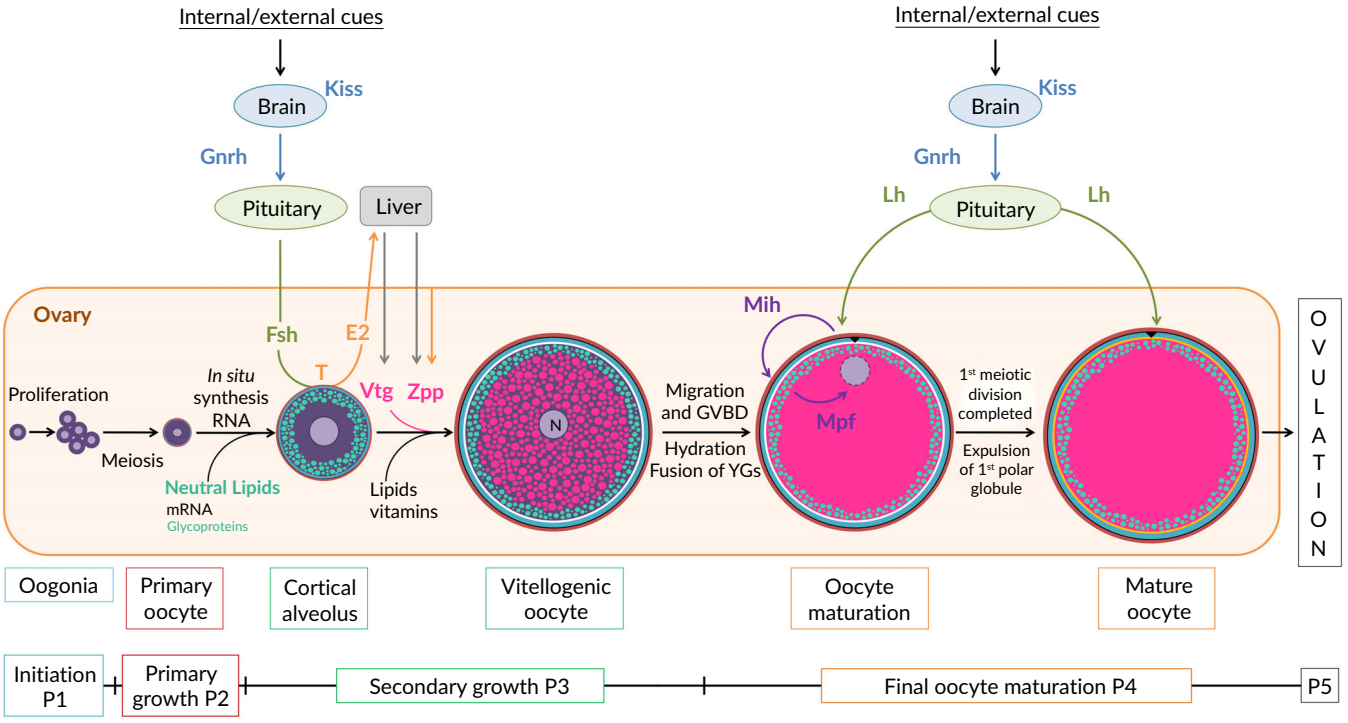

FIGURE 2 Schematic representation of oogenesis process in teleost from oogonia to mature oocyte. This figure corresponds to a generalized overview and species-specific differences exist. E2, 17β-oestradiol; Fsh, follicle stimulating hormone; Gnrh, gonadotropin releasing hormone; Kiss, kisspeptin system; Lh, luteinizing hormone; Mih, maturation inducing hormone; Mpf, maturation promoting factor; N, nucleus or germinal vesicle; T, testoster one; Vtg, vitellogenin; Zpp, zona pellucida proteins; YG, yolk granules. Redrawn from Lubzens et al. (2010) and Alix (2016). Legend: (◯) Thecal somatic layer (outer layer); (◯) Basement lamina (intermediate layer); (◯) Granulosa somatic layer (inner layer); (●) Cortical alveoli; (●) Vitellin globule/granule; (▽) Micropyle; (◯) Chorion

2 | REPRODUCTIVE DEVELOPMENT AND SPAWNING AT OPTIMAL TEMPERATURES

Gametogenesis encompasses formation, growth and maturation of germ (sex) cells (gametes) in females and males, named oogenesis and spermatogenesis, respectively. In the present work, gametogenesis in various teleost species (Supporting Information Table S1) at higher-than-optimal rather than at optimal temperatures is addressed as the latter issue has been widely reviewed (*e.g.*, Kagawa, 2013; Lubzens *et al.*, 2010, 2017; Patiño & Sullivan, 2002; Schulz *et al.*, 2010). Briefly, the main elements of gametogenesis will be introduced for a better understanding of the subsequent sections.

Oogenesis in teleosts is a dynamic process and occurs continuously in the ovary (Figure 1a), but for the sake of classification can be divided into four phases (Figures 1b and 2): (a) oogonia proliferation and transformation into a primary oocyte (PO), (b) primary or previtellogenic growth, from PO to the cortical alveoli stage (CA), (c)

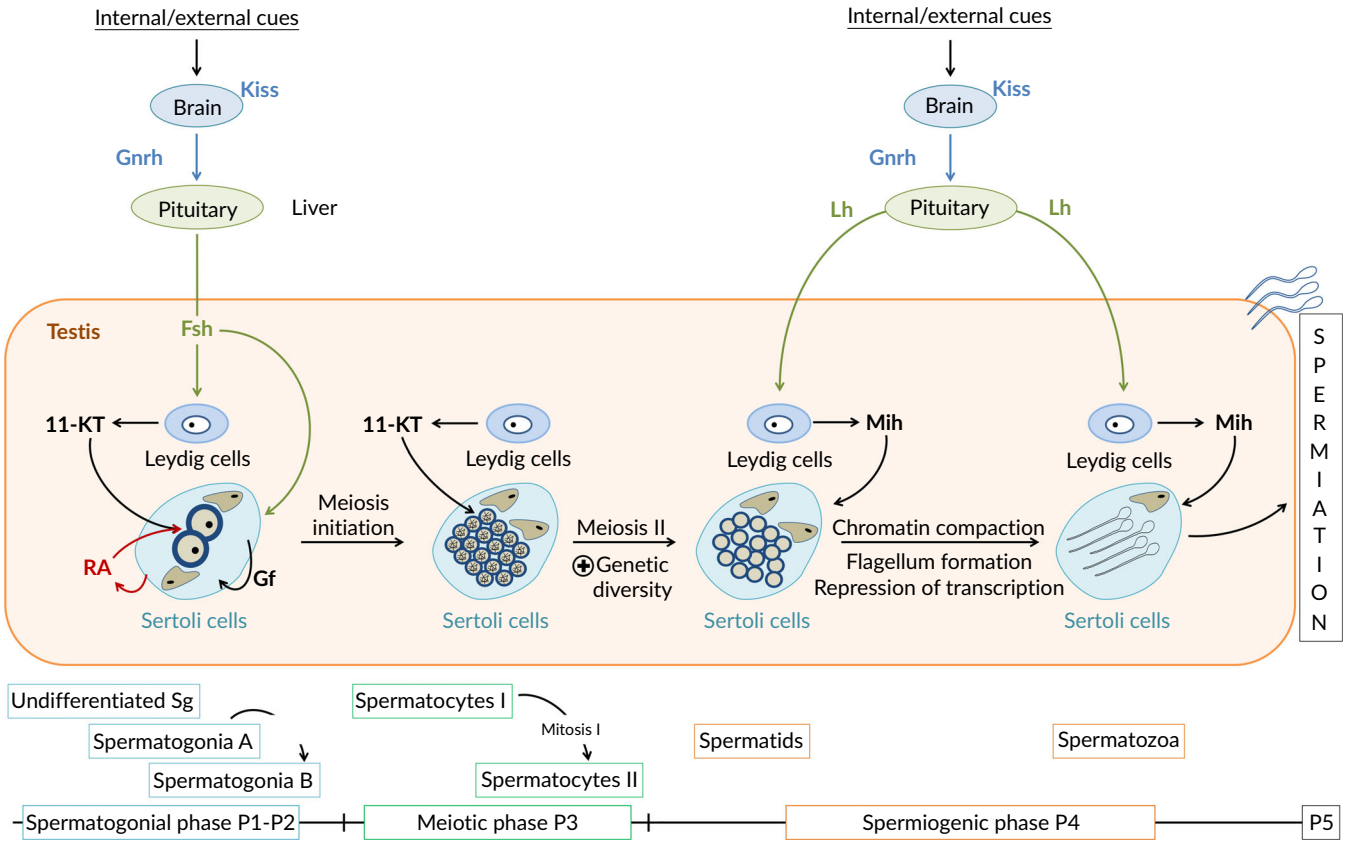

FIGURE 3 Schematic representation of spermatogenesis process in teleost from spermatogonia to spermatozoa. This figure corresponds to a generalized overview and species-specific differences exist. 11-KT, 11-ketotestosterone; Fsh, follicle stimulating hormone; Gf, growth factors; Gnrh, gonadotropin releasing hormone; Kiss, kisspeptin system; Lh, luteinizing hormone; Mih, maturation inducing hormone; RA, retinoic acid

secondary growth, the main feature of which is yolk/energy accumulation, and (d) final stages consisting of maturation (meiosis resumption), ovulation and oviposition (for review see Lubzens *et al*., 2010; Kagawa, 2013). From proliferation, the oocyte is surrounded by a monolayer of somatic granulosa cells secreting a basement lamina, and thecal somatic layer (in contact with blood vessel) which together correspond to the future follicular layer of oocyte involved in the sexual steroidogenesis for maturation and oocyte growth (Lubzens *et al*., 2010). After spawning, the empty follicle cell layer degenerates and is called a post-ovulatory follicle (POF).

In males, spermatogenesis can be divided into three phases (Figure 3): (a) the spermatogonial phase (SG) followed by (b) the meiotic phase [primary and secondary spermatocytes (Spc)] and finally (c) the spermiogenic phase ending with the production of spermatozoa (Spz) (reviewed in Schulz *et al*., 2010). This process takes place in the testes, which is composed of the germinal epithelium, corresponding mainly to somatic Sertoli cells that surround germ cells and can be organized in spermatogenic cysts (Dadras *et al*., 2019; Seivåg *et al*., 2016). Therefore, Sertoli cells continuously interact with germ cells and are essential for the support of spermatogenic cell development (*e.g*., production of growth factor and retinoic acid), survival and physiology as well as phagocytotic functions (Crespo *et al*., 2016, 2019; Schulz *et al*., 2010). Between cysts, interstitial compartments contain somatic cells and connective tissue, including blood and lymphatics vessels, Leydig cells (involved in androgen synthesis) and nerve fibres (Dadras *et al*., 2019; Domínguez-Castanedo & Uribe, 2019). The successful completion of gametogenesis results in gametes, the quality of which can be defined as the ability of spermatozoa to fertilize an ovum, or an ovum to be fertilized, resulting in the formation of a viable embryo (Bobe & Labbé, 2010).

3 | ELEVATED TEMPERATURE AND FEMALE FISH: FROM OOGENESIS TO EGG QUALITY

Higher-than-optimal temperature can act as a bottleneck for reproduction in fish species by influencing reproductive capacity and dynamics (reviewed in Pankhurst & Munday, 2011; Miranda *et al*., 2013). Such bottlenecks can be expressed at different levels, including gamete development, timing of spawning and egg quality. Timing and amplitude of thermal exposure is important as well as some periods of oogenesis may be more sensitive than others. In the following sections, the effects of higher-than-optimal temperature on oocyte development and maturation as well as spawning and egg quality are addressed.

TABLE 1 Impacts of elevated temperature on timing of spawning/ovulation/spermiation and spawning duration in males and females

Species	Spawning season	Treatment (duration – timing – temperature)	Effect	References
Ovulation or timing of spawning in females				
Alaska pollock, *Gadus chalcogrammus*	Spring	2 months – P3 to P5 – 2/5/**8°C**	Advanced	Tanaka *et al*., 2019
		Field study from 1979 to 2015		Rogers & Dougherty, 2019
Atlantic cod, *Gadus morhua*	Spring	Field study from 1985 to 2014		McQueen & Marshall, 2017
		Field study from 1999 to 2008		Kjesbu *et al*., 2010
		240 days – P6 – 5/**9°C**		
Common sole, *Solea solea*	Spring	Field study from 1970 to 2010		Fincham *et al*., 2013
Pacific cod, *Gadus macrocephalus*	Spring	Field study from 2005 to 2007		Neidetcher *et al*., 2014
Burbot *Lota lota*	Winter	21 days – P4 and P5 – 2/**4**/**6°C**		Ashton *et al*., 2019
European perch, *Perca fluviatilis*	Spring	Field study of 15 years – **+10°C**		Sandström *et al*., 1997
American yellow perch, *Perca flavescens*	Spring	5 months – P3 – 4/8/**13°C**		Feiner *et al*., 2016
Argentinian silverside, *Odontesthes bonariensis*	Spring	4 days – P3 – >20°C		Miranda *et al*., 2013
River lamprey, *Lampetra fluviatilis*	Spring	7 months – P6 – 7/10/**14°C**		Cejko *et al*., 2016
Sea trout, *Salmo trutta*	Fall/winter	4 months – P2 to P5 – 7.4/**12.4°C**	Delayed	Lahnsteiner & Leitner, 2013
Atlantic wolffish, *Anarhichas lupus*	Fall	5 months – P3 – 4/8/**12°C**		Tveiten & Johnsen, 1999, 2001
American yellow perch, *P. flavescens*	Spring	**52**/107 days – P3 – 5°C		Farmer *et al*., 2015
Arctic char, *Salvelinus alpinus*	Winter	1 month – P4 – 5/**8°C**		Gillet, 1991
Atlantic salmon, *Salmo salar*	Fall/winter	2.5 months – P3 – 14/**22°C**		Pankhurst *et al*., 2011
Atlantic salmon, *Salmo salar*		10 weeks – P3/P4 – Natural/**+5°C**	Inhibited	Vikingstad *et al*., 2016
Gobiocypris rarus	Spring to fall	60 days – P3 – 18-**30°C**		Luo *et al*., 2017
Argentinian silverside, *Odontesthes bonariensis*	Spring	8 days – P5 – 17–19/19–25/**19–27°C**		Elisio *et al*., 2012
		8 days – P4/P5 – 19/23/**27°C**		Soria *et al*., 2008
Arctic char, *S. alpinus*	Winter	3 months – P4/P5 – 5/8/**11°C**		Gillet, 1991
Lumpfish, *Cyclopterus lumpus*	Spring/summer	89 days – P4 and P5 – 6/9/**14°C** – ♀	Partially inhibited	Pountney *et al*., 2020
Spiny chromis, *Acanthochromis polyacanthus*	Spring	235 days – NA – 28.5/**30/31.5°C**	Unaffected	Donelson *et al*., 2010
Spermiation or timing of spawning in males				
Grayling, *Thymallus thymallus*	Spring	3 months – P3 to P5 – Natural/**+4°C**	Unaffected	Lahnsteiner & Kletzl, 2012
River lamprey, *L. fluviatilis*	Spring	7 months – P6 – 7/10/**14°C**		Cejko *et al*., 2016
Sea trout, *S. trutta*	Winter	4 weeks – NA – 8/**13°C**	Delayed	Fenkes *et al*., 2017
		4 months – P2 to P5 – 7.4/**12.4°C**		Lahnsteiner & Leitner, 2013
Atlantic salmon, *S. salar*	Fall/winter	10 weeks – P3/P4 – Natural/**+5°C**	Inhibited	Vikingstad *et al*., 2016
Argentinian silverside, *O. bonariensis*	Spring	8 days – P4/P5 – 19/**23/27°C**		Soria *et al*., 2008
Spawning duration				
Alaska pollock, *G. chalcogrammus*	Spring	Field study from 1979 to 2015 – ♀	Expanded	Rogers & Dougherty, 2019
Burbot, *L. lota*	Winter	21 days – P4 and P5 – 2/**4**/**6°C** – ♀	Shortened	Ashton *et al*., 2019
Sea trout, *S. trutta*	Winter	4 months – P2 to P5 – 7.4/**12.4°C** – ♂ ♀		Lahnsteiner & Leitner, 2013
Lumpfish, *C. lumpus*	Spring/summer	89 days – P4 and P5 – 6/9/**14°C** – ♀		Pountney *et al*., 2020
Atlantic wolffish, *A. lupus*	Fall	5 months – P3 – 4/8/**12°C** – ♀	Unaffected	Tveiten & Johnsen, 1999

Note: Each species is categorized as spring/summer/fall/winter spawner according to the typical timing of spawning. For each reference, the experimental protocol utilized is briefly described. Treatment: bold lettering indicates the temperature(s) at which "Effects" were observed. P1 to P6 correspond to different phases of gametogenesis. For females: P1, initiation; P2, primary growth; P3, secondary growth; P4, final maturation; P5, spawning; P6, oogenesis (no specific phase identified). For males: P1–P2, spermatogonial phase; P3, meiotic phase; P4, spermiogenic phase; P5, spawning; P6, spermatogenesis (no specific phase identified). For spawning duration, impacts of high temperature on males (♂) and females (♀) are indicated in the "Treatment" column. Abbreviation: NA, no information available.

3.1 | Oocyte development

During oogenesis, rising temperature can accelerate gamete maturation and oocyte growth as shown in grayling [*Thymallus thymallus* (L. 1758)] (Lahnsteiner & Kletzl, 2012) and *G. morhua*, and oocyte recruitment appears more effective with an increased production of POs (Kjesbu *et al*., 2010). However, fish responses are also dependent on the amplitude and timing of thermal rise, and elevated temperature can also slow gamete growth, sometimes up to arrest oocyte maturation (Lahnsteiner & Kletzl, 2012; Luo *et al*., 2017). For example, short exposure to elevated temperature enhances the gonadosomatic index (GSI, *i.e*., gonad weight related to fish weight) in three-spine stickleback (*Gasterosteus aculeatus* L.), yet prolonged exposure results in a GSI decrease, probably due to emergence of atresia (Hani *et al*., 2019). Similar results to those in *G. aculeatus* have been reported in the European bullhead (*Cottus gobio* L.) exposed to control and warm temperatures (14°C or 18°C relative to 10°C). Deleterious effects were observed at higher temperature such as stagnated GSI, small oocyte diameter and high pre-ovulatory atresia (Dorts *et al*., 2012). Nonetheless, the increase to 14°C accelerated oogenesis and resulted in an early GSI peak and larger oocyte diameter, but also a higher proportion of atretic follicles (Dorts *et al*., 2012). In the Atlantic wolffish (*Anarhichas lupus* L.), high temperature during secondary growth delayed vitellogenesis, leading to a shift in final oocyte maturation (FOM) (Tveiten & Johnsen, 2001). Vikingstad *et al*. (2016) reported changes in un-ovulated (end of spawning season) oocyte morphology (*e.g*., large variation in size, misshape and uneven colour of oocytes) in the Atlantic salmon (*Salmo salar* L.) subjected to warm temperatures during the 10 last weeks of oogenesis. The authors associated these changes with the atresia process during gametogenesis (Vikingstad *et al*., 2016). On the contrary, in the spiny chromis [*Acanthochromis polyacanthus* (Bleeker 1855)], the relationship between temperature and vitellogenic oocyte proportion was weak, suggesting that warmer-than-optimal water did not have a critical impact on *A. polyacanthus* oogenesis within the temperature range tested (30°C and 31.5°C). Despite this weak relationship, egg size was smaller at the higher temperature (Donelson *et al*., 2010). Depending on the species and the characteristics of the thermal insult, elevated temperature can affect the progression of oocyte development resulting, in the worst cases, in resorption of oocytes.

3.2 | FOM, ovulation and spawning

FOM appears to be highly thermally sensitive and developmental events that occur at this time can affect egg quality. Among the reproductive dysfunctions associated with elevated temperature exposure during FOM, ovary morphological abnormalities (*e.g*., cavity in the ovary membrane), variability in oocyte maturation or increased prevalence of atresia have been observed. In wild Atlantic herring (*Clupea harengus* L.), ovary abnormalities and misshapen vitellogenic (VO)/FOM oocytes were common, probably related to high water temperature (upper limit during FOM), which may impair egg release and lead to reproductive impairment (Ojaveer *et al*., 2015). High temperature during the spawning season results in the same defects as reported in pikeperch [*Sander lucioperca* (L. 1758)] (Hermelink *et al*., 2013). Resorbing oocytes in wild common dace (*Leuciscus leuciscus* L.) during the spawning season could be due to rapid fluctuations of temperature during FOM (Nowosad *et al*., 2014). Atretic structures were also reported in the Argentinian silverside [*Odontesthes bonariensis* (Valenciennes 1835)] subjected to high constant or fluctuating temperatures (sometimes encountered in the natural environment) during FOM and spawning (23°C and 27°C *vs*. 19°C) (Elisio *et al*., 2012; Soria *et al*., 2008). Unlike *C. harengus*, oogenesis advanced when the temperature was reduced to the control level following thermal exposure in *O. bonariensis* (Elisio *et al*., 2012; Ojaveer *et al*., 2015). As a result of the various maturation issues described, ovulation rate decreases, as found in many species across taxa, for example freshwater bream *Abramis brama* L., *O. bonariensis*, and *S. salar* (Elisio *et al*., 2012; Targońska *et al*., 2014; Vikingstad *et al*., 2016).

3.2.1 | Overripening

The process of overripening is influenced by temperature, which is of particular importance to aquaculture due to the implications for egg quality (Mohagheghi Samarin *et al*., 2015; Valdebenito *et al*., 2015). For example, in Arctic char [*Salvelinus alpinus* (L. 1758)], females maintained at 8°C presented a faster decrease in ova fertility than fish at 5°C (Gillet, 1991). The deleterious effect of overripening on egg developmental success was faster in rainbow trout [*Oncorhynchus mykiss* (Walbaum 1792)] females maintained at 17°C relative to those at 12°C (Aegerter & Jalabert, 2004). In the same species, individuals kept at higher-than-optimal temperature (20°C *vs*. 8°C) during maturation and spawning displayed oocytes with an overripened appearance (translucent with a red spot) in the ovarian tissue (Davies & Bromage, 2002). In addition, the quality of ovulated eggs deteriorated at a faster rate in *Rutilus kutum* (Kamensky 1901) held at 14°C relative to 11°C (Samarin *et al*., 2011). Thus, overripening appears to be faster in warmer water, causing egg quality to decrease more rapidly.

3.2.2 | POF dynamics

POF prevalence and aging is important for spawning frequency estimation as an intrinsic part of spawning stock biomass assessments by egg production methods (EPMs), a common technique used worldwide on predominately small pelagics (Bernal *et al*., 2012). POF absorption is a temperature-dependent process, as demonstrated in captive Atlantic menhaden [*Brevoortia tyrannus* (Latrobe 1802)], where POFs were difficult to distinguish after 36 h of maintenance at 19–20°C, and resorption was less advanced at 15–18°C (Fitzhugh & Hettler, 1971). Similarly, in wild Iberian pilchard [*Sardina pilchardus* (Walbaum 1792)], POFs shrank approximately 3% faster per 1°C increase in temperature (Ganias *et al*., 2007). Given that incorrectly estimating the age of POFs can lead to bias in reproductive (EPM-

based) assessments of wild fish (Ganias *et al*., 2007), a deeper understanding of the POF–temperature relationship and improved biological forecasting is needed. This is especially relevant for migratory species with potentially complex thermal histories, such as the cold-water fish *G. morhua*. In *G. morhua*, POFs can persist for many months (Witthames *et al*., 2010) and their presence has been used to establish maturity ogives (age- or length-at-sexual maturity) (Saborido-Rey & Junquera, 1998) and to gauge the prevalence of skipped spawners (Skjæraasen *et al*., 2012). Therefore, temperature-induced changes in post-ovulatory dynamics may have implications for reproductive capacity and other fisheries-related estimates.

3.3 | Timing of ovulation and spawning

3.3.1 | Captive fish

Climate-related phenological shifts in reproductive season have been observed in several taxa such as amphibians, reptiles and birds, and the larger influential stressor among climatic variables seems to be the temperature (Cohen *et al*., 2018). After exposure of captive females to high temperature, spawning season onset or peak can be delayed, advanced, unchanged or even inhibited (Table 1 and Figure 4) (Donelson *et al*., 2010; Gillet, 1991; Lahnsteiner & Leitner, 2013; Miranda *et al*., 2013; Tanaka *et al*., 2019; Tveiten & Johnsen, 2001; Vikingstad *et al*., 2016). These differences in term of phenology could be partly dependent on the timing or duration of exposure as shown in American yellow perch [*Perca flavescens* (Mitchill 1814)] in which shortening winter period (*i.e*., temperature increase above 5°C during FOM) delays spawning season (Farmer *et al*., 2015) whereas high temperature (13°C *vs*. 4°C for 5 months) during secondary growth leads to advanced spawning season (Feiner *et al*., 2016). On the contrary, in *A. lupus*, ovulation is delayed after thermal exposure during secondary growth or FOM (Tveiten *et al*., 2001; Tveiten & Johnsen, 2001).

Partial or complete inhibition of ovulation has been observed across taxa, when temperature thresholds are exceeded (Table 1) (Donelson *et al*., 2010; Gillet, 1991; Luo *et al*., 2017; Pountney *et al*., 2020; Soria *et al*., 2008; Vikingstad *et al*., 2016). Interestingly, when *S. alpinus* are transferred from 8°C to 5°C, thermal recovery was observed, that is, ovulation was stimulated and synchronized (Gillet, 1991). A similar protocol has also been used in *S. salar* to induce ovulation (King *et al*., 2007). On the contrary, in the tropical species *A. polyacanthus*, unchanged timing of spawning for fish facing elevated temperatures could be interpreted as a lack of plasticity. Together with the decrease in the proportion of successfully reproducing fish (*i.e*., complete failure of reproduction) at high temperatures, this may lead to a decline of coral reef fish populations as suggested by Donelson *et al*. (2010). Miranda *et al*. (2013) proposed a scheme in which effects of elevated temperature during fish vitellogenesis were divided in two categories, early or delayed breeding season in spring or fall spawners, respectively. However, if critical thresholds are exceeded in terms of thermal amplitude or duration of exposure, this rule will not apply as the collective result is inhibition of ovulation (Donelson *et al*., 2010; Gillet, 1991; Luo *et al*., 2017; Soria *et al*., 2008; Vikingstad *et al*., 2016). In addition, spawning frequency can also change in response to elevated temperature. For example, in *Gobiocypris rarus* Ye & Fu 1983, spawning frequency tends to decrease as long as thermal conditions increase above the optimum (Luo *et al*., 2017). Finally, in *P. flavescens*, the proportion of actively spawning females increased after exposure to the highest temperature tested (13°C relative to 4°C or 8°C, temperatures reflect inter-annual differences during winter for wild fish) during secondary growth probably to counteract the decrease in egg quality and average fecundity (Feiner *et al*., 2016).

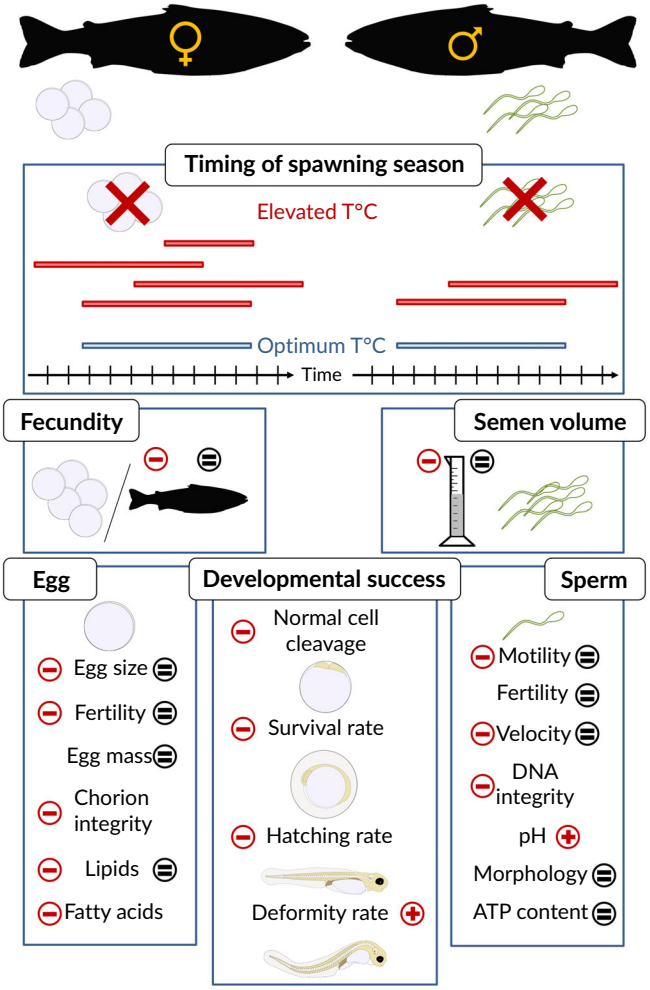

FIGURE 4 Summary of impacts of elevated temperature on reproductive performance in males and females. In the 'Timing of spawning season' inset, the blue and red bands correspond to the spawning season (timing and duration) at optimum or higher-than-normal temperatures, respectively. The spawning season can be unchanged, delayed, advanced and/or shortened. The absence of spawning season is represented by the red cross. Negative sign reflects a negative effect or a decrease in the criteria response, positive sign to an increase whereas equal sign to no measurable impact. For some criteria, several effects have been identified depending on species and/or amplitude/timing of exposure

3.3.2 | Wild populations

Long-term temperature changes experienced by individuals can have a significant impact on spawning grounds or timing of reproductive events (spawning, migration) (reviewed in Drinkwater *et al*., 2010). Thus, phenological changes due to rising temperatures are already documented in wild populations, and are variable depending on the species or even the populations (Table 1) (Kjesbu *et al*., 2010; McQueen & Marshall, 2017; Poloczanska *et al*., 2013; Rogers & Dougherty, 2019; Sandström *et al*., 1997). For example, in European perch (*Perca fluviatilis* L.), the spawning period was advanced by 1 month, and was extended in individuals exposed during their entire life cycle (about 15 years) to warm effluent water (about 10°C above ambient temperature) (Sandström *et al*., 1997). Moreover, for the same populations, the spawning season was extended compared to reference areas (Sandström *et al*., 1997). Similarly, in populations of Alaska pollock (*Gadus chalcogrammus* Pallas 1814), earlier and longer spawning season were partly associated with higher SST, especially during FOM (Rogers & Dougherty, 2019). The authors highlighted nonlinearities in fish responses to temperature, for example advance in spawning date in warm waters until a threshold, after which additional temperature increase had no impact (Rogers & Dougherty, 2019). In *G. morhua*, spawning season is advanced due to faster oocyte rate development in warmer water (Kjesbu *et al*., 2010). This phenological shift has been observed in the Irish Sea (0.9 weeks decade^{-1}) and North Sea (0.8–2.4 weeks decade^{-1}) between 1985 and 2014 in association with autumn SST (McQueen & Marshall, 2017). In the same regions between 1970 and 2010, the common sole [*Solea solea* (L. 1758)] spawning season reflected a shift to earlier reproductive events as well (Fincham *et al*., 2013).

These phenological shifts are particularly important as they dictate the biotic and abiotic conditions to which offspring will be exposed. Consequently, larval survival could be impacted due to mismatch with prey (plankton) abundance or proper size spectrum, for example due to delayed spawning time, inducing starvation or slower growth (Asch *et al*., 2019; Farmer *et al*., 2015; Hillebrand *et al*., 2018; Tanaka *et al*., 2019). Moreover, a shortened spawning season as in burbot [*Lota lota* (L. 1758)] leads to a narrower temporal window for hatching (Ashton *et al*., 2019). This suggests that shifts of reproductive events could potentially lead to changes in recruitment and population dynamics in temperate fishes, a phenomenon that is projected to increase in the context of climate change (Asch *et al*., 2019). However, not all species can adapt and shift their reproductive season due to their reliance on cues, such as photoperiod, for the timing of spawning (Hansen *et al*., 2001; Wang *et al*., 2010). Therefore, the scope for adjusting this timing may be limited for some species (Farmer *et al*., 2015). Additionally, it appears as though phenology may also be latitude-dependent (*e.g*., tropical species). Indeed, Cohen *et al*. (2018) demonstrated that, for animals in general, different climate variables, such as precipitation, can influence phenology.

3.4 | Fecundity at spawning

Observed fecundity is probably the most widely used indicator of reproductive fitness in recruitment studies (Grazer & Martin, 2012; Kjesbu, 2016). Throughout the reproductive cycle, fecundity may be reduced by atresia, that is, so-called "down-regulation", or dynamically increased due to *de novo* recruitment of developing oocytes (Kjesbu, 2016). Under global warming and increasing atresia, lowered fecundity could be expected. Nonetheless, in unfavourable environments, oogonial mitotic division can be stimulated, potentially inducing an increase of fecundity (*e.g*., *Prochilodus argenteus* Spix & Agassiz 1829) (Thomé *et al*., 2012). Thereby, relative fecundity at spawning (egg/g body weight) and potential fecundity do not seem to be affected by thermal breeder exposure [*e.g*., Sea trout (*S. trutta* L.), *A. lupus*, *P. flavescens* and *L. lota*] (Ashton *et al*., 2019; Farmer *et al*., 2015; Feiner *et al*., 2016; Lahnsteiner & Leitner, 2013; Tveiten *et al*., 2001; Tveiten & Johnsen, 1999). However, in *S. salar*, *O. bonariensis* and river lamprey [*Lampetra fluviatilis* (L. 1758)], evidence of depression of relative fecundity has been found (Anderson *et al*., 2017a; Cejko *et al*., 2016; Elisio *et al*., 2012; Pankhurst *et al*., 2011). Taken together, increased oogonial proliferation and increased atresia might be expected to operate in different fecundity directions in warming waters, meaning that predicting the resulting fecundity would require in-depth species-specific studies.

3.5 | Temperature and egg quality

It is commonly accepted that higher-than-optimal temperatures negatively impact a range of parameters that collectively dictate egg quality (Table 2). Below, we sequentially cover the impacts of high temperature on the most studied factors, namely egg morphology, biochemical and molecular composition, fertility and subsequent early developmental success of offspring.

3.5.1 | Egg morphology

Contradictory results have been reported regarding the impact of high temperature on egg size, ranging from no effect to reduced egg diameter, associated sometimes with increasing intra-clutch variance (Ashton *et al*., 2019; Donelson *et al*., 2010; Farmer *et al*., 2015; Feiner *et al*., 2016; Fuxjäger *et al*., 2019; King *et al*., 2003; Tanaka *et al*., 2019; Tveiten *et al*., 2001; Tveiten & Johnsen, 1999) (Table 2). Similar to the timing of spawning, the moment at which parents are exposed to elevated temperature can modulate impacts on egg size. In *A. lupus*, eggs from fish exposed during secondary growth had reduced size (Tveiten & Johnsen, 1999), whereas individuals facing high temperatures during FOM did not (Tveiten & Johnsen, 2001), suggesting that egg size in *A. lupus* is determined before FOM. Changes in egg size may lead to variation of offspring size and thereby potentially negatively influence fitness (Feiner *et al*., 2016), depending on species and whether egg size and developmental success are correlated (Brooks *et al*., 1997).

TABLE 2 Impacts of elevated temperature during oogenesis on subsequent egg quality in various fish species

Criteria	Species	Treatment (duration – timing – temperature)	Effect	References
Fertility	*Gobiocypris rarus*	60 days – P3 – 18-**30°C**	Reduced	Luo *et al*., 2017
	Atlantic salmon, *Salmo salar*	3 months – P3 – 14/18/**22°C**		King *et al*., 2003
	Sea trout, *Salmo trutta*	4 months – P2 to P5 – 7.4/**12.4°C**		Lahnsteiner & Leitner, 2013
	Argentinian silverside, *Odontesthes bonariensis*	4 days – P3 (early/mid/late vtg) – >20°C		Miranda *et al*., 2013
	Atlantic cod, *Gadus morhua*	NA – P6 – <9.6/**>9.6°C**		van der Meeren & Ivannikov, 2006
	Three-spine stickleback, *Gasterosteus aculeatus*	120 days – NA – 16/18/**21°C**	Reduced[a]	Hani *et al*., 2019
	Atlantic salmon, *S. salar*	2.5 months – P3 – 14/**22°C**	Reduced[b]	Pankhurst *et al*., 2011
	Atlantic wolffish, *Anarhichas lupus*	5 months – P3 – 4/8/**12°C**	Unaffected	Tveiten & Johnsen, 1999
		14 days – P4 and P5 – 4/8/**12°C**		Tveiten *et al*., 2001
Developmental success				
Normal cell cleavage	Atlantic wolffish, *A. lupus*	14 days – P4 and P5 – 4/8/**12°C**	Abnormal	Tveiten *et al*., 2001
	Atlantic cod, *Gadus morhua*	NA – P6 – <9.6/**>9.6°C**		van der Meeren & Ivannikov, 2006
Survival rate	Three-spine stickleback, *G. aculeatus*	120 days – NA – 16/18/**21°C**	Reduced	Hani *et al*., 2019
	Atlantic salmon, *S. salar*	3 months – P3 – 14/18/**22°C**		King *et al*., 2003
	Grayling, *Thymallus thymallus*	3 months – P3 to P5 – Natural/**+4°C**		Lahnsteiner & Kletzl, 2012
	Burbot, *Lota lota*	21 days – P4 and P5 – 2/**4**/**6°C**		Ashton *et al*., 2019
	Freshwater bream, *Abramis brama*	10 days – P5 – 20.5/**21.2**/**23.5°C**		Targońska *et al*., 2014
	Atlantic wolffish, *A. lupus*	14 days – P4 and P5 – 4/8/**12°C**		Tveiten *et al*., 2001
	Rainbow trout, *Oncorhynchus mykiss*	6 weeks – P4 – 12/**17°C**	Reduced[b]	Colson *et al*., 2019
	Atlantic salmon, *S. salar*	2.5 months – P3 – 14/**22°C**		Pankhurst *et al*., 2011
	Atlantic wolffish, *A. lupus*	5 months – P3 – 4/8/**12°C**	Reduced [a]	Tveiten & Johnsen, 1999
Hatching rate	*G. rarus*	60 days – P3 – 18-**30°C**	Reduced	Luo *et al*., 2017
	Three-spine stickleback, *G. aculeatus*	120 days – NA – 16/18/**21°C**		Hani *et al*., 2019
	American yellow perch, *Perca flavescens*	**52**/107 days – P3 – 5°C		Farmer *et al*., 2015
	Atlantic wolffish, *A. lupus*	14 days – P4 and P5 – 4/8/**12°C**	Reduced [a]	Tveiten *et al*., 2001
Deformity rate	*G. rarus*	60 days – P3 – 18-**30°C**	Increased	Luo *et al*., 2017
	Burbot, *L. lota*	21 days- P4 and P5 – 2/**4**/**6°C**		Ashton *et al*., 2019
	Freshwater bream, *Abramis brama*	10 days – P5 – 20.5/**21.2**/**23.5°C**		Targońska *et al*., 2014
	Rainbow trout, *O. mykiss*	6 weeks – P4 – 12/**17°C**	Unaffected	Colson *et al*., 2019
Larval length	American yellow perch, *P. flavescens*	**52**/107 days – P3 – 5°C	Reduced	Farmer *et al*., 2015
Offspring behaviour	Rainbow trout, *O. mykiss*	6 weeks – P4 – 12/**17°C**	Affected	Colson *et al*., 2019
Egg morphology				
Egg size	Spiny chromis, *Acanthochromis polyacanthus*	235 days – NA – 28.5/**30**/**31.5°C**	Reduced	Donelson *et al*., 2010
	Atlantic wolffish, *A. lupus*	5 months – P3 – 4/8/**12°C**		Tveiten & Johnsen, 1999
	American yellow perch, *P. flavescens*	**52**/107 days – P3 – 5°C		Farmer *et al*., 2015
	Three-spine stickleback, *G. aculeatus*	18 days – P5 – 17/**21°C**		Fuxjäger *et al*., 2019
	Alaska pollock, *Gadus chalcogrammus*	2 months – P3 to P5 – 2/5/**8°C**	Reduced[b]	Tanaka *et al*., 2019
	American yellow perch, *P. flavescens*	5 months – P3 – 4/8/**13°C**	Unaffected	Feiner *et al*., 2016
	Burbot, *L. lota*	21 days – P4 and P5 – 2/**4**/**6°C**		Ashton *et al*., 2019
	Atlantic wolffish, *A. lupus*	14 days – P4 and P5 – 4/8/**12°C**		Tveiten *et al*., 2001
Chorion integrity	Atlantic salmon, *S. salar*	3 months – P3 – 14/18/**22°C**	Damaged	King *et al*., 2003
Jelly membrane integrity	European perch, *Perca fluviatilis*	P0 – Natural/**+10°C**	Damaged	Sandström *et al*., 1997

(Continues)

TABLE 2 (Continued)

Criteria	Species	Treatment (duration – timing – temperature)	Effect	References
Egg mass (mg)	American yellow perch, *P. flavescens*	5 months – P3 – 4/8/**13°C**	Unaffected	Feiner *et al*., 2016
	Sea trout, *S. trutta*	4 months – P2 to P5 – 7.4/**12.4°C**		Lahnsteiner & Leitner, 2013
	Grayling, *T. thymallus*	3 months – P3 to P5 – Natural/**+4°C**		Lahnsteiner & Kletzl, 2012
	River lamprey, *Lampetra fluviatilis*	7 months – P6 – 7/10/**14°C**		Cejko *et al*., 2016
Egg biochemical and molecular composition				
FA composition	American yellow perch, *P. flavescens*	5 months – P3 – 4/8/**13°C**	Affected	Feiner *et al*., 2016
FA levels	Sea trout, *S. trutta*	4 months – P2 to P5 – 7.4/**12.4°C**	Reduced	Lahnsteiner & Leitner, 2013
Lipid content (mg/egg)	American yellow perch, *P. flavescens*	**52**/107 days – P3 – 5°C	Reduced	Farmer *et al*., 2015
		5 months – P3 – 4/8/**13°C**	Unaffected	Feiner *et al*., 2016
	Sea trout, *S. trutta*	4 months – P2 to P5 – 7.4/**12.4°C**		Lahnsteiner & Leitner, 2013
DHA/AA/EPA	American yellow perch, *P. flavescens*	5 months – P3 – 4/8/**13°C**	Unaffected	Feiner *et al*., 2016
Protein concentration	Sea trout, *S. trutta*	4 months – P2 to P5 – 7.4/**12.4°C**		Lahnsteiner & Leitner, 2013
Total carbohydrates				
Lysozyme activity				
Maternal mRNA content	Rainbow trout, *O. mykiss*	6 weeks – P4 – 12/**17°C**	Affected	Colson *et al*., 2019

Note: Details as for Table 1.
Abbreviations: AA, arachidonic acid; DHA, docosahexaenoic acid; EPA, eicosapentaenoic acid; FA, fatty acid; NA, no information available.
[a]A nonstatistically significant trend.
[b]The effect can vary depending on the experimental conditions tested.

Other aspects of egg morphology appear to be impacted by warm water exposure, such as the chorion. The chorion of unfertilized eggs from thermally exposed *S. salar* had "blister-like holes" (King *et al*., 2003). Incidence of chorion damage was weakly but significantly negatively correlated with survival rates at the eyed-egg stage, and it is apparent that the damage was present prior to ovulation (King *et al*., 2003). In *P. fluviatilis*, egg quality has been reported to decrease in fish exposed to water about 10°C above ambient temperature, and egg ribbons from these individuals started to disintegrate shortly after fertilization (Sandström *et al*., 1997). Females exposed to high temperature seemed unable to produce an adequate jelly membrane to provide adhesion between the eggs. Damage to this structure could lead to high mortality during embryogenesis as eggs seems to be susceptible to infections (Sandström *et al*., 1997).

3.5.2 | Egg biochemical and molecular composition

Among biochemical components, imbalances in egg fatty acids (FA) could affect early embryo development and survival as FAs are involved in numerous cellular functions such as cell construction and fluidity to energy storage and use (Wiegand, 1996). Even though less information is available about egg biochemical composition in the context of global warming, FAs appear to be modulated by temperature in different species (Feiner *et al*., 2016; Lahnsteiner & Leitner, 2013). For example, after maternal exposure to high temperature, FA levels (free or total) decreased, and FA composition (*e.g*., proportion of docosahexaenoic, linoleic and palmitoleic acids) was affected in *P. flavescens* (Lahnsteiner & Leitner, 2013). Lipid content can also be negatively affected by higher-than-optimal temperature or not depending on species and studies (Table 2) (Farmer *et al*., 2015; Feiner *et al*., 2016; Lahnsteiner & Leitner, 2013). Timing of exposure is also a consideration within-species (*e.g*., *P. flavescens*), as are photoperiod and maternal nutritional status (Farmer *et al*., 2015; Feiner *et al*., 2016; Miranda *et al*., 2013).

To our knowledge, only one study has investigated the impact of temperature on the egg transcriptome. In this recent study, significant differences in mRNA content were noted in unfertilized eggs from *O. mykiss* females exposed to elevated temperature (17°C relative to 12°C) (Colson *et al*., 2019). Among the differentially accumulated transcripts detected, some are involved in fish neurodevelopment (*aust2*, *dpysl5*) or related to human cognitive disorders (*arv1*, *plp2*) and their dysregulation may contribute to offspring behaviour (see below) (Colson *et al*., 2019).

3.5.3 | Egg fertility and developmental success

The decrease in fertilization rate observed following maternal exposure to elevated temperature is a common tendency among species (King *et al*., 2003; Lahnsteiner & Leitner, 2013; Miranda *et al*., 2013; Pankhurst *et al*., 2011; van der Meeren & Ivannikov, 2006) (Table 2), even though there are exceptions (*e.g*., *A. lupus*, Tveiten & Johnsen, 1999; Tveiten *et al*., 2001). The timing of female exposure to

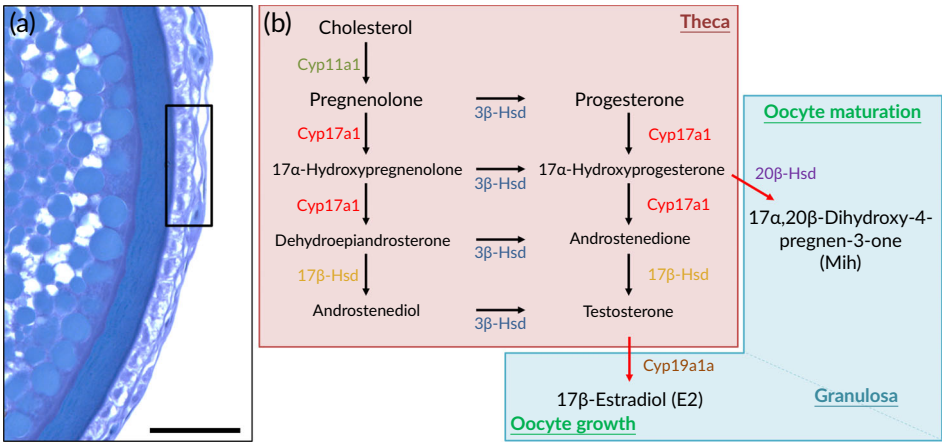

FIGURE 5 (a) The theca and granulosa layer (black square) in a vitellogenic oocyte. Scale bar: 50 μm. (b) The two-cell type model of ovarian steroidogenesis. *Cyp11a1*, p450 cholesterol side-chain cleavage protein; *Cyp17a1*, 17α-hydroxylase/C17,20-lyase; 3β-Hsd, 3β-hydroxysteroid dehydrogenase; 17β-Hsd, 17β-hydroxysteroid dehydrogenase; 20β-hsd, 20β-hydroxysteroid dehydrogenase; Cyp19a1a, p450 aromatase

high temperatures appears important. For example, negative consequences on fertilization were recorded in females that experienced elevated temperature at the end of secondary growth (*i.e.*, mid- and late vitellogenesis) while no effect has been observed in females treated at the beginning of the vitellogenesis (Miranda *et al.*, 2013). Higher-than-optimal temperatures experienced by the females negatively impacts developmental success by, for instance, reducing survival, hatching rate and increasing abnormal development (*e.g.*, abnormal cell cleavage), as well as deformity rates of newly hatched larvae, regardless of duration or timing of thermal exposure (Table 2) (Ashton *et al.*, 2019; Colson *et al.*, 2019; Hani *et al.*, 2019; King *et al.*, 2003; Lahnsteiner & Leitner, 2013; Luo *et al.*, 2017; Targońska *et al.*, 2014; Tveiten *et al.*, 2001; Tveiten & Johnsen, 1999; van der Meeren & Ivannikov, 2006). Moreover, a recent work revealed the relationship between maternal exposure to elevated temperature and offspring behaviour. Fry originating from *O. mykiss* females exposed to higher-than-optimal temperature (17°C *vs.* 12°C) were less reactive to challenging situation, and slower in swimming and in the spatial learning tasks, suggesting an impaired emotional reactivity and learning deficit (Colson *et al.*, 2019). These disorders may be associated with dysregulation of particular maternal mRNA as mentioned above, and could impact wild fish survival as well as fish welfare in aquaculture.

In spite of common trends of temperature-mediated negative effect on egg quality, only a few parameters are commonly investigated. In particular, for the relationship between emerging indicators (*e.g.*, proteomic or transcriptomic profiles), there has been no or only one study characterizing the impact of high temperature on the fish egg proteome and transcriptome respectively. These elements could help us decipher the mechanisms underlying developmental success in that context and this field is an area for future research. To complete results obtained by work at the group level (*i.e.*, aggregated response of several fish) and understand better the origins of the reduction in egg quality, it would be interesting to perform individual tracking studies and multiple sampling throughout the reproductive cycle until spawning to associate individual reproductive performance (*e.g.*, egg quality) with oogenesis progress.

4 | IMPACTS OF ELEVATED TEMPERATURE ON REPRODUCTIVE PHYSIOLOGY IN FEMALES

In fish, reproductive processes are controlled by the BPG axis, which is a complex endocrine cascade involving many genes, receptors, enzymes and hormones (Roa *et al.*, 2008; Zohar *et al.*, 2010). While it is apparent that no single cue is responsible for "switching on" the BPG axis; stimuli may come in the form of genetic, metabolic or environmental signals (Liu *et al.*, 2017; Roa *et al.*, 2008), and the collective result is stimulation of the endocrine cascade, progression through gametogenesis and production of viable gametes. In this section, our purpose is not to provide an in-depth review of the complex (and sometimes controversial) molecular pathways involved in the regulation of reproduction. Rather, we will give an overview of how higher-than-optimal temperatures influence the physiological rhythms and processes that occur from primary growth to ovulation and spawning. For reference, a generalized overview of the BPG axis in females and a more detailed depiction of ovarian steroidogenesis in optimal conditions are given in Figures 2 and 5, respectively. The temperature-related impacts covered in the following sections are also summarized in Table 3.

4.1 | Primary and secondary growth

Many aspects of temperature-induced physiological impairment are poorly understood; however it is clear that impacts may be felt at all levels of the reproductive endocrine cascade, and expressed differently depending on the species, degree of thermal insult, stage of ovarian development and nutritional status, among other things. For example, at the time of writing, we were not able to find studies detailing how the kisspeptin (Kiss) system responds to elevated temperature in female fish. However, progress has been made for other regulating factors at the level of the brain and pituitary. For example, expression of gonadotropin-releasing hormone (Gnrh) gene *gnrh1* (but not *gnrh2* or *gnrh3*) was reduced in response to higher temperatures

TABLE 3 Impacts of elevated temperature on female reproductive physiology

Criteria	Species name	Treatment (duration – timing – temperature)	Effect	References
Plasma levels				
T	Atlantic wolffish, *Anarhichas lupus*	5 months – P3 – 4/8/**12°C**	Reduced	Tveiten & Johnsen, 2001
	Senegalese sole, *Solea senegalensis*	2.5 years – P6 – Natural/**constant 18/20°C**		García-López *et al*., 2006
	Atlantic salmon, *Salmo salar*	2.5 months – P3 – 14/**22°C**		Pankhurst *et al*., 2011
	Argentinian silverside, *Odontesthes bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**		Elisio *et al*., 2012
		8 days – P4/P5 – 19/**23/27°C**		Soria *et al*., 2008
	European bullhead, *Cottus gobio*	14 weeks – P4/P5 – 6-10/10–14/**14–18°C**		Dorts *et al*., 2012
	Hippocampus erectus	4 weeks – NA – 22/26/**30°C**	Unaffected	Qin *et al*., 2018
E2	Atlantic salmon, *S. salar*	10 weeks – P3/P4 – Natural/**+5°C**	Reduced	Vikingstad *et al*., 2016
		4 to 6 weeks – P6 – 14/**22°C**		King *et al*., 2007
		2.5 months – P3 – 14/**22°C**		Pankhurst *et al*., 2011
	Argentinian silverside, *O. bonariensis*	8 days – P4/P5 – 19/**23/27°C**		Soria *et al*., 2008
	Pikeperch, *Sander lucioperca*	4 months – NA – 12/14/16/**18°C**		Hermelink *et al*., 2013
	European bullhead, *C. gobio*	14 weeks – P4/P5 – 6-10/10–14/**14–18°C**		Dorts *et al*., 2012
	Hapuku wreckfish, *Polyprion oxygeneios*	2 years – P6 – variable 10–17°C/**constant 17°C**		Wylie *et al*., 2018
	Fire clownfish, *Amphiprion melanopus*	NA – P5 – 28.5/30/**31.5°C**		Miller *et al*., 2015
	Atlantic wolffish, *A. lupus*	5 months – P3 – 4/8/**12°C**		Tveiten & Johnsen, 2001
	Japanese seabream, *Pagrus major*	10 days – P5 – 17/**24°C**		Okuzawa & Gen, 2013
	Three-spine stickleback, *Gasterosteus aculeatus*	15 days – NA – 16/18/**21°C**		Hani *et al*., 2019
	Senegalese sole, *S. senegalensis*	2.5 years – P6 – Natural/**constant 18/20°C**		García-López *et al*., 2006
	European eel, *Anguilla anguilla*	6 weeks – P6 – 10-15/15–18/**18°C**		Mazzeo *et al*., 2014
		4 weeks – P6 – 10/**20°C**		Pérez *et al*., 2011
	H. erectus	4 weeks – NA – 22/26/**30°C**	Unaffected	Qin *et al*., 2018
Vtg	Atlantic salmon, *S. salar*	4 to 6 weeks – P6 – 14/**22°C**	Reduced	King *et al*., 2007
	European bullhead, *C. gobio*	14 weeks – P4/P5 – 6-10/10–14/**14–18°C**		Dorts *et al*., 2012
	Striped bass, *Morone saxatilis*	400 days – P6 – Natural/**constant 18°C**		Clark *et al*., 2005
	Three-spine stickleback, *G. aculeatus*	15 days – NA – 16/18/**21°C**	Increased	Hani *et al*., 2019
Mih	Atlantic salmon, *S. salar*	10 weeks – P3/P4 – Natural/**+5°C**	Reduced	Vikingstad *et al*., 2016
	Arctic char, *Salvelinus alpinus*	40 days – P4/P5 – 5/**10°C**		Gillet *et al*., 2011
	Atlantic wolffish, *A. lupus*	5 months – P3 – 4/8/**12°C**		Tveiten *et al*., 2000
Gene expression				
gnrh1	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Reduced	Elisio *et al*., 2012
	Japanese seabream, *P. major*	5/10 days – P5 – 17/**24°C**		Okuzawa & Gen, 2013
gnrh2	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Unaffected	Elisio *et al*., 2012
gnrh3	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Unaffected	Elisio *et al*., 2012
	Three spot gourami, *Trichogaster trichopterus*	9 days – NA – 23/27/**31°C**	Reduced or unaffected	Levy *et al*., 2011
gnrhr	Japanese seabream, *P. major*	5/10 days – P5 – 17/**24°C**	Reduced	Okuzawa & Gen, 2013
fshβ	Argentinian silverside, *O. bonariensis*	8 days – P4/P5 – 19/**23/27°C**	Unaffected	Soria *et al*., 2008
	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Reduced	Elisio *et al*., 2012
	Japanese seabream, *P. major*	5 days – P5 – 17/**24°C**		Okuzawa & Gen, 2013
	European eel, *A. anguilla*	4 weeks – P6 – 10/**20°C**		Pérez *et al*., 2011
	Three spot gourami, *T. trichopterus*	9 days – NA – 23/27/**31°C**	Increased[a]	Levy *et al*., 2011
lhβ	Japanese seabream, *P. major*	10 days – P5 – 17/**24°C**	Reduced	Okuzawa & Gen, 2013

TABLE 3 (Continued)

Criteria	Species name	Treatment (duration – timing – temperature)	Effect	References
	Argentinian silverside, *O. bonariensis*	8 days – P4/P5 – 19/**23/27°C**		Soria *et al*., 2008
		8 days – P5 – 17-19/19–25/**19–27°C**	Unaffected	Elisio *et al*., 2012
	Atlantic salmon, *S. salar*	4 months – P3 – Ambient/**+2°C**	Delayed	Taranger *et al*., 2015
fshr	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Reduced	Elisio *et al*., 2012
		8 days – P4/P5 – 19/**23/27°C**		Soria *et al*., 2008
	Coho salmon, *Oncorhynchus kisutch*	24 h – P3 *in vitro* – 14/**22°C**		Anderson *et al*., 2019
	Atlantic salmon, *S. salar*	4 months – P3 – Ambient/**+2°C**	Unaffected	Taranger *et al*., 2015
		3 months – P3 – 14/**22°C**		Anderson *et al*., 2017a
lhr	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Reduced	Elisio *et al*., 2012
	Argentinian silverside, *O. bonariensis*	8 days – P4/P5 – 19/**23/27°C**	Unaffected	Soria *et al*., 2008
	Coho salmon, *O. kisutch*	24 h – P3 *in vitro* – 14/**22°C**		Anderson *et al*., 2019
	Atlantic salmon, *S. salar*	4 months – P3 – Ambient/**+2°C**		Taranger *et al*., 2015
star	Atlantic salmon, *S. salar*	3 months – P3 – 14/**22°C**	Unaffected	Anderson *et al*., 2017a
Cyp11a1	Atlantic salmon, *S. salar*	3 months – P3 – 14/**22°C**	Reduced	Anderson, Swanson, *et al*., 2012
cyp19a1a	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Reduced	Elisio *et al*., 2012
	European eel, *A. anguilla*	6 weeks – P6 – 10-15/15–18/**18°C**		Mazzeo *et al*., 2014
	Coho salmon *O. kisutch*	24 h – P3 *in vitro* – 14/**22°C**		Anderson *et al*., 2019
	Atlantic salmon, *S. salar*	3 months – P3–14/**22°C**		Anderson, Swanson, *et al*., 2012
foxl2	Atlantic salmon, *S. salar*	3 months – P3 – 14/**22°C**	Unaffected	Anderson *et al*., 2017a
3β-hsd	Atlantic salmon, *S. salar*	3 months – P3 – 14/**22°C**	Unaffected	Anderson *et al*., 2017a
	Coho salmon, *O. kisutch*	24 h – P3 *in vitro* – 14/**22°C**		Anderson *et al*., 2019
Cyp17a1	Coho salmon, *O. kisutch*	24 h – P3 *in vitro* – 14/**22°C**	Reduced	Anderson *et al*., 2019
erα	European eel, *A. anguilla*	4 weeks – P6–10/**20°C**	Reduced[a]	Pérez *et al*., 2011
	Atlantic salmon, *S. salar*	3 months – P3 – 14/**22°C**	Unaffected	Anderson, Swanson, *et al*., 2012
vtg	Pool barb, *Puntius sophore*	60 days – NA – 27/**36°C**	Reduced	Mahanty *et al*., 2019
	Atlantic salmon, *S. salar*	2.5 months – P3 – 14/**22°C**		Pankhurst *et al*., 2011
	European eel, *A. anguilla*	4 weeks – P6 – 10/**20°C**	Reduced[a]	Pérez *et al*., 2011
	Fathead minnow, *Pimephales promelas*	2 months – P3 – 12/16/**20°C**	Increased	Firkus *et al*., 2018
zpb	Atlantic salmon, *S. salar*	2.5 months – P3 – 14/**22°C**	Reduced	Pankhurst *et al*., 2011
zpc	Atlantic salmon, *S. salar*	2.5 months – P3 – 14/**22°C**	Reduced	Pankhurst *et al*., 2011

Note: Details as for Table 1.

Abbreviations: *Cyp11a1*, p450 cholesterol side-chain cleavage protein; *Cyp17a1*, 17α-hydroxylase/C17,20-lyase, Cyp19a1a: p450 aromatase; E2, 17β-estradiol; Erα, E2 receptor; foxl2, forkhead transcription factor L2; Fsh, follicle stimulating hormone; Fshr, Fsh receptor; Gnrh, gonadotropin releasing hormone; Gnrhr, Gnrh receptor; Lh, luteinizing hormone; Lhr, Lh receptor; Mih, maturation inducing hormone; NA, no information available; star, steroidogenic acute regulatory protein; T, testosterone; Vtg, vitellogenin; Zpb and Zpc: zona pellucida; 3β-Hsd: 3β-hydroxysteroid dehydrogenase.

[a]The effect can vary depending on the experimental conditions tested.

(fluctuation of 17–19°C *vs*. 19–25°C) in *O. bonariensis* during advanced vitellogenesis (Elisio *et al*., 2012), though at constant temperature (12°C *vs*. 20°C) expression of all three brain *gnrhs* was unaffected (Miranda *et al*., 2009). In vitellogenic three-spot gourami [*Trichogaster trichopterus* (Pallas 1770)] maintained in the presence of nest-building males, *gnrh3* was not impacted by an increase in temperature from 27°C to 31°C (Levy *et al*., 2011). Interestingly, when females were kept without males, expression of *gnrh3* was suppressed at 31°C, suggesting that social cues modulate the impact of temperature (Levy *et al*., 2011).

Downstream of *gnrh*, down-regulation of pituitary follicle stimulating hormone (Fsh) gene *fshβ* has been noted for some species (Elisio

TABLE 4 Impacts of elevated temperature during spermatogenesis on sperm quality and seminal plasma in various fish species

Criteria	Species name	Treatment (duration –timing – temperature)	Effect	References
Semen volume	Sea trout, *Salmo trutta*	4 months – P2 to P5 – 7.4/**12.4°C**	Unaffected	Lahnsteiner & Leitner, 2013
	Argentinian silverside, *Odontesthes bonariensis*	4 days – P4 – >20°C		Miranda *et al*., 2013
	River lamprey, *Lampetra fluviatilis*	7 months – P6 – 7/10/**14°C**		Cejko *et al*., 2016
	Grayling, *Thymallus thymallus*	3 months – P3 to P5 – Natural/**+4°C**	Affected	Lahnsteiner & Kletzl, 2012
	Burbot, *Lota lota*	21 days – P4 and P5 – 2/**4/6°C**	Reduced	Ashton *et al*., 2019
	Freshwater bream, *Abramis brama*	10 days – P5–20.5/**21.2/23.5°C**		Targońska *et al*., 2014
Sperm density	Lumpfish, *Cyclopterus lumpus*	89 days – P4 and P5 – 6/9/**14°C**	Reduced	Pountney *et al*., 2020
Sperm fertility	Sea trout, *S. trutta*	4 months – P2 to P5 – 7.4/**12.4°C**	Unaffected	Lahnsteiner & Leitner, 2013
Sperm motility	Sea trout, *S. trutta*	4 months – P2 to P5 – 7.4/**12.4°C**	Unaffected	
	Grayling, *T. thymallus*	3 months – P3 to P5 – Natural/**+4°C**	Affected	Lahnsteiner & Kletzl, 2012
	River lamprey, *L. fluviatilis*	7 months – P6 – 7/10/**14°C**	Reduced	Cejko *et al*., 2016
	Freshwater bream, *A. brama*	10 days – P5 – 20.5/**21.2/23.5°C**		Targońska *et al*., 2014
Sperm velocity	River lamprey, *L. fluviatilis*	7 months – P6 – 7/10/**14°C**	Reduced	Cejko *et al*., 2016
	Sea trout, *S. trutta*	4 months – P2 to P5 – 7.4/**12.4°C**	Unaffected	Lahnsteiner & Leitner, 2013
	Sea trout, S. trutta	4 weeks – NA – 8/**13°C**	Reduced[a]	Fenkes *et al*., 2017
DNA integrity	Sea trout, *S. trutta*	4 months – P2 to P5 – 7.4/**12.4°C**	Reduced	Lahnsteiner & Leitner, 2013
Sperm pH	River lamprey, *L. fluviatilis*	7 months – P6 – 7/10/**14°C**	Increased	Cejko *et al*., 2016
Seminal plasma				
Osmolality	River lamprey, *L. fluviatilis*	7 months – P6 – 7/10/**14°C**	Unaffected	Cejko *et al*., 2016
pH	River lamprey, L. fluviatilis	7 months – P6 – 7/10/**14°C**	Increased	Cejko *et al*., 2016
Total protein content	River lamprey, L. fluviatilis	7 months – P6 – 7/10/**14°C**	Unaffected	Cejko *et al*., 2016
Peroxidase	Sea trout, *S. trutta*	4 months – P2 to P5 – 7.4/**12.4°C**	Reduced	Lahnsteiner & Leitner, 2013
Lysozyme activity	Sea trout, *S. trutta*	4 months – P2 to P5 – 7.4/**12.4°C**	Reduced	
Spermatozoa energy metabolism				
ATP concentration	Sea trout, *S. trutta*	4 months – P2 to P5 – 7.4/**12.4°C**	Unaffected	Lahnsteiner & Leitner, 2013
Spermatozoa morphology				
Sperm total length	Sea trout, *S. trutta*	4 weeks – NA – 8/**13°C**	Unaffected	Fenkes *et al*., 2019
Flagellum length, FL				
Flagellar deformity rate				
Sperm head length, HL				
Head width				
Head surface area, HSA				
FL/HL				
FL/HSA	Sea trout, *S. trutta*	4 weeks – NA – 8/**13°C**	Increased	Fenkes *et al*., 2019

Note: Details as for Table 1.
Abbreviation: NA, no information available.
[a]The effect can vary depending on the experimental conditions tested.

et al., 2012; Pérez *et al*., 2011; Veilleux *et al*., 2018), though there are exceptions, such as *T. trichopterus* females maintained with reproductively active males (Levy *et al*., 2011). Interestingly, *S. salar* reared at 22°C have higher levels of plasma Fsh relative to those at 14°C in the months preceding ovulation (Anderson, Swanson, *et al*., 2012). As these fish are estradiol (E2)-compromised, it is thought that a lack of

TABLE 5 Impacts of elevated temperature male reproductive physiology

Criteria	Species name	Treatment (duration – timing – temperature)	Effect	References
Plasma levels				
T	European bullhead, *Cottus gobio*	14 weeks – P4/P5 – 6-10/10–14/**14–18°C**	Reduced	Dorts *et al*., 2012
	Striped bass, *Morone saxatilis*	400 days – P6 – Natural/**constant 18°C**		Clark *et al*., 2005
	Argentinian silverside, *Odontesthes bonariensis*	8 days – P4/P5 – 19/**23/27°C**		Soria *et al*., 2008
	Pikeperch, *Sander lucioperca*	4 months – NA – 12/14/16/**18°C**		Hermelink *et al*., 2013
	Atlantic salmon, *Salmo salar*	10 weeks – P3/P4 – Natural/**+5°C**		Vikingstad *et al*., 2016
11-KT	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Reduced	Elisio *et al*., 2012
	Atlantic salmon, *S. salar*	10 weeks – P3/P4 – Natural/**+5°C**		Vikingstad *et al*., 2016
	Pikeperch, *S. lucioperca*	4 months – NA – 12/14/16/**18°C**		Hermelink *et al*., 2013
	Striped bass, *M. saxatilis*	400 days – P6 – Natural/**constant 18°C**		Clark *et al*., 2005
	European bullhead, *C. gobio*	14 weeks – P4/P5 – 6-10/10–14/**14–18°C**		Dorts *et al*., 2012
	Spiny chromis, *Acanthochromis polyacanthus*	235 days – NA – 28.5/**30/31.5°C**	No increase[b]	Donelson *et al*., 2010
Mih	Atlantic salmon, *S. salar*	10 weeks – P3/P4 – Natural/**+5°C**	Reduced	Vikingstad *et al*., 2016
Gene expression				
kiss1	Zebra danio, *Danio rerio*	7 days – NA – 27/**35°C**	Unaffected	Shahjahan *et al*., 2013
kiss2	*Takifugu niphobles*	7 days – P5 – 21/**28°C**	Reduced	Shahjahan *et al*., 2017
	Zebra danio, *D. rerio*	7 days – NA – 27/**35°C**		Shahjahan *et al*., 2013
kiss2r	*T. niphobles*	7 days – P5 – 21/**28°C**	Reduced	Shahjahan *et al*., 2017
gnrh1	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Reduced	Elisio *et al*., 2012
	T. niphobles	7 days – P5 – 21/**28°C**		Shahjahan *et al*., 2017
gnrh2	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Unaffected	Elisio *et al*., 2012
	T. niphobles	7 days – P5 – 21/**28°C**		Shahjahan *et al*., 2017
	Zebra danio, *D. rerio*	7 days – NA – 27/**35°C**		Shahjahan *et al*., 2013
gnrh3	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Unaffected	Elisio *et al*., 2012
	T. niphobles	7 days – P5 – 21/**28°C**		Shahjahan *et al*., 2017
	Three spot gourami, *Trichogaster trichopterus*	9 days – NA – 27/**31°C**	Reduced	David & Degani, 2011
	Zebra danio, *D. rerio*	7 days – NA – 27/**35°C**		Shahjahan *et al*., 2013
fshβ	Argentinian silverside, *O. bonariensis*	8 days – P4/P5 – 19/**23/27°C**	Reduced[a]	Soria *et al*., 2008
	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Reduced	Elisio *et al*., 2012
	T. niphobles	7 days – P5 – 21/**28°C**		Shahjahan *et al*., 2017
	Three spot gourami, *T. trichopterus*	9 days – NA – 27/**31°C**	Unaffected	David & Degani, 2011
lhβ	Argentinian silverside, *O. bonariensis*	8 days – P4/P5 – 19/**23/27°C**	Reduced[a]	Soria *et al*., 2008
	Argentinian silverside, *O. bonariensis*	8 days – P5 – 17-19/19–25/**19–27°C**	Reduced	Elisio *et al*., 2012
	T. niphobles	7 days – P5 – 21/**28°C**		Shahjahan *et al*., 2017
	Three spot gourami, *T. trichopterus*	9 days – NA – 27/**31°C**	Unaffected	David & Degani, 2011
fshr	Argentinian silverside, *O. bonariensis*	8 days – P4/P5 – 19/23/27°C	Unaffected	Soria *et al*., 2008
		8 days – P5 – 17-19/19–25/19–27°C		Elisio *et al*., 2012
lhr	Argentinian silverside, *O. bonariensis*	8 days – P4/P5 – 19/23/27°C	Unaffected	Soria *et al*., 2008
		8 days – P5 – 17-19/19–25/19–27°C		Elisio *et al*., 2012

Note: Details as for Table 1.

Abbreviations: 11-KT, 11-ketotestosterone; Fsh, follicle stimulating hormone; Fshr, Fsh receptor; Gnrh, gonadotropin releasing hormone; kiss, kisspeptin system; kissr, kiss receptor; Lh, luteinizing hormone; Lhr, Lh receptor; Mih, maturation inducing hormone; NA, no information available; T, testosterone.

[a]A nonstatistically significant trend.

[b]The effect can vary depending on the experimental conditions tested.

negative feedback by E2 on Fsh synthesis may be to blame (Anderson, Swanson, *et al*., 2012). Reproductive performance in maiden spawning fish, that is, gamete quality and eyed-egg survival was severely reduced at the higher temperature (Pankhurst *et al*., 2011) despite high levels of circulating Fsh, raising an important question concerning whether temperature-induced endocrine dysfunction can occur directly at the level of the gonad, independently of events occurring in the brain and pituitary as previously suggested by Lim *et al*. (2003) and Pankhurst and King (2010).

Lower levels of circulating testosterone (T) have been reported for several salmonid and nonsalmonid species reared at higher-than-optimal temperatures (Dorts *et al*., 2012; Elisio *et al*., 2012; García-López *et al*., 2006; Pankhurst *et al*., 2011; Tveiten & Johnsen, 2001), and following warm conditions in wild populations (Flett *et al*., 1996). Similarly, circulating E2 levels are typically reduced at high temperatures across taxonomic groups (Table 3) (Hermelink *et al*., 2013; King *et al*., 2007; Mazzeo *et al*., 2014; Miller *et al*., 2015; Okuzawa & Gen, 2013; Pérez *et al*., 2011; Soria *et al*., 2008; Tveiten & Johnsen, 2001; Vikingstad *et al*., 2016; Wylie *et al*., 2018). However, there are exceptions where exposure to high temperatures had no apparent impact on circulating steroid levels, or the impacts on the endocrine system were inconsistent. In *Hippocampus erectus* Perry 1810, 1 month of chronic thermal stress at 30°C did not impair E2 and T plasma levels relative to other groups at 22°C and 26°C, even though mortality and basal metabolic rate increased (Qin *et al*., 2018). Furthermore, in *O. mykiss* the impacts on steroid production were inconsistent between years, with the depression of circulating E2 present in some years and not others (Pankhurst *et al*., 1996; Pankhurst & Thomas, 1998).

Multiple mechanisms have been proposed to explain the observed reductions in circulating gonadal steroids at high temperatures. Beginning near the top of the BPG axis, a dampening of the Gnrh/Fsh system could contribute to reproductive dysfunction, as the ovary may suffer from a lack of stimulation to produce E2 (Elisio *et al*., 2012). In addition, this problem would theoretically be exacerbated by reduced ovarian Fsh receptor (*fshr*) expression, a temperature-induced feature of some teleost species (Anderson *et al*., 2019; Elisio *et al*., 2012). On the other hand, exposure to elevated temperature did not significantly impact *fshr* in *S. salar* during peak-vitellogenesis (Anderson *et al*., 2017a), and in this species E2 levels are severely reduced at high temperatures despite high levels of circulating Fsh (Anderson, Swanson, *et al*., 2012). Thus, the impacts of exposure to elevated temperature on genes involved in gonadal steroidogenesis must be considered in adult fish, especially since thermal modulation of steroidogenic genes is considered crucial for temperature-dependent sex determination during earlier life-cycle stages (Caruso *et al*., 2016; He *et al*., 2016).

Undoubtedly the best-studied steroidogenic enzyme is Cyp19a1a, expression of which appears to be thermally sensitive in all adult fish species studied thus far (Table 3) (Anderson *et al*., 2019; Anderson, Swanson, *et al*., 2012; Elisio *et al*., 2012; Mazzeo *et al*., 2014). Studies on teleosts have strongly implicated forkhead transcription factor L2 (*foxl2*) in the down-regulation of Cyp19a1a since it is thermally sensitive during sex differentiation, and plays a role in Cyp19a1a (and 17α-hydroxylase/C17,20-lyase, *Cyp17a1*) transcription (Wang *et al*., 2007; Yamaguchi *et al*., 2007; Zhou *et al*., 2007). However, in *S. salar*, there is no evidence to suggest *foxl2* is thermally sensitive during vitellogenesis (Anderson *et al*., 2017a), and this is the only study to date looking at the expression of this gene in response to temperature in adult fish. Furthermore, while aromatase activity appears to be closely linked to gonadal development in fish (Lee *et al*., 2001; Young *et al*., 1983), studies on Cyp19a1a enzyme activity in adult fish are lacking in the context of temperature exposure.

In addition to Cyp19a1a, there are a suite of steroidogenic enzymes and other proteins that, if thermally sensitive, have the potential to influence E2 production. For example, the transport of cholesterol by the steroidogenic acute regulatory protein (Star) across the inner mitochondrial membrane is a crucial step in ovarian steroidogenesis (Lubzens *et al*., 2010), yet expression of this gene does not appear to be thermally sensitive during early or peak-vitellogenesis in *S. salar* (Anderson *et al*., 2017a). In addition, expression of 3β-hydroxysteroid dehydrogenase (*3β-hsd*) appears to be similarly uncompromised at high temperature during early vitellogenesis in coho salmon [*Oncorhynchus kisutch* (Walbaum 1792)] *in vitro* (Anderson *et al*., 2019), and during mid-vitellogenesis in *S. salar* (Anderson *et al*., 2017a). In contrast, *Cyp11a1* (p450 cholesterol side-chain cleavage protein) is strongly depressed during the later stages of vitellogenesis in *S. salar* (Anderson, Swanson, *et al*., 2012), and *Cyp17a1* is depressed by high temperature in *O. kisutch* primary growth follicles *in vitro* (Anderson *et al*., 2019). The molecular basis for reduced *Cyp11a1* and *Cyp17a1* is currently unclear. However, it is likely that compromised expression of *fshr*, *Cyp11a1*, *Cyp17a1* and other genes higher on the endocrine cascade contributes to a lack of available substrate for E2 production, and these effects may be exacerbated by impairment of Cyp19a1a activity and gene expression.

Impairment of E2 production at higher temperatures has the downstream consequence of reducing vitellogenin (Vtg)/*vtg* levels as observed across taxonomic groups (Table 3) (Clark *et al*., 2005; Dorts *et al*., 2012; Mahanty *et al*., 2019; Pankhurst *et al*., 2011; Pérez *et al*., 2011). However, in species such as *G. aculeatus* and fathead minnow (*Pimephales promelas* Rafinesque 1820), *vtg*/Vtg production is stimulated by warm temperature (Firkus *et al*., 2018; Hani *et al*., 2019). While the zona pellucida (Zp) synthesis at high temperature has received less attention than Vtg, thermal inhibition hepatic *zpb* and *zpc* has been demonstrated for *S. salar* during vitellogenesis, although the impacts on *zpb* were more severe (Pankhurst *et al*., 2011).

As E2 driven synthesis of Vtg and Zp is down-regulated at high temperature, it is important to consider whether this may be due to issues at the E2 receptor (Er) level. A study on adult *S. salar* demonstrated that hepatic *erα* is not thermally sensitive at any time during vitellogenesis (Anderson, Swanson, *et al*., 2012), whereas suppressed *erα* was observed during early vitellogenesis in European eel [*Anguilla anguilla* (L. 1758)] (Pérez *et al*., 2011). In addition to expression, the negative effects of high temperature on Er binding affinity have been demonstrated for both *S. salar* (Watts *et al*., 2005) and blue tilapia [*Oreochromis aureus* (Steindachner 1864)] (Tan *et al*., 1999). Despite

this, hepatic tissue appears to maintain E2 responsiveness in terms of Vtg synthesis and the accumulation of nuclear Ers (Anderson *et al*., 2017b; Anderson, King, et al., 2012; Körner *et al*., 2008; Mackay & Lazier, 1993). In fact, the rate of E2 utilization, subsequent Vtg synthesis and sequestration of Vtg into the ovary is often more rapid with increased temperature (Anderson, King, *et al*., 2012; Mackay & Lazier, 1993; Tyler *et al*., 1987). However, this may not be the case for other E2 responsive genes, such as those belonging to the Zp family. For example, in juvenile *S. salar*, hepatic *zpb* (and to a lesser extent *zpc*) transcription was reduced in E2-treated fish maintained at 22°C relative to 14°C (Anderson, King, *et al*., 2012), while adult fish maintained at 22°C did not respond to E2 treatment at all in terms of *zpb* and *zpc* expression during vitellogenesis (Anderson *et al*., 2017b). Thus, it is likely that lower Vtg/*vtg* levels occur mostly as a result of reduced E2 tone, and not reductions in Er binding affinity. There is also evidence to suggest that temperature may have differential effects on Vtg and Zp synthesis, though this is yet to be studied in nonsalmonids.

4.2 | Maturation, ovulation and spawning

Delay or complete inhibition of FOM and ovulation, and therefore spawning, appear to be caused by thermal inhibition of physiological processes in the brain, pituitary and/or ovary. For example, the expression of *gnrh1* and its receptor (*gnrhr*) are lower in Japanese seabream (*Pagrus major* Temminck & Schlegel 1843) following short-term exposure to elevated temperature during the spawning season (Okuzawa & Gen, 2013). Somewhat surprisingly, in captive *O. mykiss* and wild *O. kisutch* circulating luteinizing hormone (Lh) was not affected by elevated temperature, even though maturation, ovulation and egg quality were negatively impacted (Flett *et al*., 1996; Pankhurst *et al*., 1996). However, in *S. salar* thermal challenge caused a delay in the *lhβ* peak (Taranger *et al*., 2015), which could have been interpreted as a decrease in expression if only one time point was sampled. As mentioned elsewhere, the timing of sampling is crucial when aiming to quantify Lh as it relates to FOM/ovulation in salmonids (Anderson, Swanson, *et al*., 2012). In nonsalmonids such as *P. major* and *O. bonariensis*, reductions in *lhβ* and/or *lhr* expression have been observed during the spawning season (Elisio *et al*., 2012; Okuzawa & Gen, 2013; Soria *et al*., 2008) and thermally induced dopaminergic inhibition at the level of the pituitary may be involved (Glasser *et al*., 2004).

In terms of gonadal steroidogenesis, impairment of maturation inducing hormone (Mih, 17α, 20β-dihydroxy-4-pregnen-3-one or 17α,20β,21-trihydroxy-4-pregnen-3-one, depending on the species) synthesis has been demonstrated for the salmonids *S. alpinus*, *S. salar* and *O. kisutch* (Flett *et al*., 1996; Gillet *et al*., 2011; Vikingstad *et al*., 2016) and the nonsalmonid *A. lupus* (Tveiten *et al*., 2000) during the latter stages of reproductive development. It is not clear what the molecular basis is for reduced synthesis of Mih. However, *Cyp11a1* was down-regulated approximately 1 month before ovulation in *S. salar* maintained at high temperature (Anderson, King, *et al*., 2012), and ovarian tissue appears to be less responsive to hormonal signals with increasing temperature across taxa (Drori *et al*., 1994; Glasser *et al*., 2004; King & Pankhurst, 2004).

5 | ELEVATED TEMPERATURE AND MALE FISH: FROM SPERMATOGENESIS TO SPERM QUALITY

Although fewer works have investigated the impacts of warmer-than-optimal temperature on male than female reproductive development and gamete quality, some trends appear consistent between the species studied. For example, in several species elevated temperature causes a partial or complete gonadal regression (decrease in or lower GSI, and arrested development) (de Siqueira-Silva *et al*., 2015; Dorts *et al*., 2012; Elisio *et al*., 2012, 2015; Hani *et al*., 2019; Shahjahan *et al*., 2017). High temperature has also been associated with a reduction in early-stage gamete proportion (Spg and Spc) in several species, reflecting a lack of capacity to initiate spermatogenesis, associated with GSI decrease, for example in *O. bonariensis* exposed to high but natural temperature fluctuations (Elisio *et al*., 2012). In the same species, constant high temperature at the end of spermatogenesis diminished Spz number (Soria *et al*., 2008), and similar observations have been made in *A. polyacanthus* exposed to 1.5°C and 3°C warmer than reference (Donelson *et al*., 2010). Spz density was also reduced in lumpfish (*Cyclopterus lumpus* L.) exposed to high temperature (14°C relative to 6°C or 9°C) (Pountney *et al*., 2020). Collectively, thermally driven changes during spermatogenesis can result in a lower number of spermiating males, reduction in Spz quantity (suggested by Dorts *et al*., 2012; Hani *et al*., 2019) and thus a reduction in semen volume across several taxa (Table 4 and Figure 4) (Ashton *et al*., 2019; Lahnsteiner & Kletzl, 2012; Targońska *et al*., 2014). Apoptosis process could partly explain the decrease in semen production observed in some species (Ashton *et al*., 2019; Lahnsteiner & Kletzl, 2012). On the contrary, in species such as *O. bonariensis*, *S. trutta* and *L. fluviatilis*, semen volume is not impacted by temperature (Cejko *et al*., 2016; Lahnsteiner & Leitner, 2013; Miranda *et al*., 2013).

In addition to spermatogenesis, the spermiation initiation and duration can be influenced by temperature (Table 1 and Figure 4). In *S. trutta*, timing and duration of spawning was delayed and shortened, respectively (Fenkes *et al*., 2017; Lahnsteiner & Leitner, 2013), following a 5°C temperature increase. On the contrary, in *L. fluviatilis* and *T. thymallus*, both spring spawners, no change in spawning timing was reported after a thermal treatment (Cejko *et al*., 2016; Lahnsteiner & Kletzl, 2012). In *O. bonariensis* and *S. salar*, elevated temperatures (27°C and 23°C *vs*. 19°C, and natural temperature +5°C, respectively) completely inhibited semen production (Soria *et al*., 2008; Vikingstad *et al*., 2016). Changes in spawning timing and duration for males could have consequences for the reproductive performance of fish populations, as spawning may no longer be synchronized with females, whose spawning may have also shifted.

5.1 | Temperature and sperm quality

Although sperm performance seems to be affected by warmer-than-optimal conditions, results vary depending on the species, duration and amplitude of exposure (Table 4).

5.1.1 | Sperm motility and velocity

Male exposure to warm temperatures during the meiotic and spermiogenic phase affects male reproductive potential and, depending on the species, sperm motility can be impaired (Cejko *et al*., 2016; Lahnsteiner & Kletzl, 2012; Targońska *et al*., 2014) or remain unchanged (Lahnsteiner & Leitner, 2013) (Table 4 and Figure 4). In a recent study on *S. trutta*, cumulative effects of high temperature during spermatogenesis (4 weeks at 13°C relative to 8°C) and sperm activation caused a decrease in sperm velocity, without impacting the proportion of motile cells at the beginning of spawning (Fenkes *et al*., 2017). However, later in the spawning season, the temperature-driven difference in sperm quality was no longer present (Fenkes *et al*., 2017). In another study on *S. trutta*, no change in sperm velocity was observed when males were exposed for a longer time (4 months, 12.4°C relative to 7.4°C) (Lahnsteiner & Leitner, 2013). The authors suggested that delayed sperm maturation in warm acclimated males could induce issues in sperm swimming speed (Fenkes *et al*., 2017). In contrast, a reduction in sperm velocity was observed after a thermal challenge in *L. fluviatilis* (Cejko *et al*., 2016). Sperm motility and velocity corresponded to the sperm's ability to reach the egg, and negative effects of temperature on these two criteria could induce fertilization issues.

5.1.2 | Additional considerations for sperm quality

Additional criteria such as morphology and metabolism underpin the ability of sperm to reach the egg. High temperature did not negatively impact sperm morphological parameters (*e.g*., flagellum length, total length), cause flagellar deformity (Fenkes *et al*., 2019) or change ATP content (Lahnsteiner & Leitner, 2013) in *S. trutta*. However, Spz DNA integrity decreased with increased temperature (Lahnsteiner & Leitner, 2013). Similar results have been observed in Senegalese sole (*Solea senegalensis* Kaup 1858) in which DNA fragmentation increased from spring until reaching a maximum in June, suggesting that fragmentation could be related to increasing water temperature (Beirão *et al*., 2011). Finally, biochemical composition of seminal plasma can be modified by temperature. For example, seminal plasma lysozyme and peroxidase activity was reduced in *S. trutta* (Lahnsteiner & Leitner, 2013), whereas pH increased in *L. fluviatilis* and osmolality was unchanged (Cejko *et al*., 2016) in response to elevated temperature. In addition, exposure of sperm to high temperature immediately following spawning can lead to negative effects on sperm quality (reviewed by Dadras *et al*., 2017). However, few studies have investigated cumulative effects of high temperature during maturation and post-spawning on sperm quality (Fenkes *et al*., 2017, 2019), and more research in this area is needed. Taken together, these studies demonstrate that higher-than-optimal temperature can negatively impact sperm quality. Combined with the changes in spawning timing and the reductions in male output discussed above, this may lead to a decrease in reproductive success and a diminished ability of male fish to fertilize eggs as water temperature increases.

6 | IMPACTS OF ELEVATED TEMPERATURE ON REPRODUCTIVE PHYSIOLOGY IN MALES

As for females, reproductive development in males is controlled by the BPG axis, which can be negatively impacted by higher-than-optimal temperatures. For reference, a generalized overview of the endocrine cascade in optimal conditions appears in Figure 3, and the temperature impacts on male reproductive physiology, with a focus on the spermiogenic and spawning phases, are discussed below and summarized in Table 5.

The higher levels of the reproductive endocrine cascade, namely Kisspeptin/Gnrh/gonadotropins (Gths), can be impacted by warm temperatures. For instance, in *Takifugu niphobles* (Jordan & Snyder 1901), brain gene expression of *kiss2* and its receptors *kiss2r* were reduced at 28°C relative to 21°C (Shahjahan *et al*., 2017). Brain expression of *gnrh1* was also reduced at higher temperature, whereas *gnrh2* was not affected in several species (Elisio *et al*., 2012; Shahjahan *et al*., 2013, 2017). Responses of brain *gnrh3* to high water temperature may also vary, as there was no effect in *O. bonariensis* and *T. niphobles* (Elisio *et al*., 2012; Shahjahan *et al*., 2017) but suppression occurred in the Zebra danio [*Danio rerio* (Hamilton 1822)] and *T. trichopterus* (David & Degani, 2011; Shahjahan *et al*., 2013). Downstream, high temperature did not impact *fshβ* or *lhβ* subunits in *T. trichopterus* maintained in reproductive conditions (David & Degani, 2011), nor did it impact expression of these genes in *O. bonariensis* (though there was a nonsignificant tendency for lower expression) (Soria *et al*., 2008). However, pituitary levels of *lhβ* and *fshβ* decreased significantly in *T. niphobles* and *O. bonariensis* reared at elevated temperature (Elisio *et al*., 2012; Shahjahan *et al*., 2017), but expression of *lhr* and *fshr* in the testes was not affected in *O. bonariensis* (Elisio *et al*., 2012; Soria *et al*., 2008). Circulating androgen [T, 11-ketotestosterone (11-KT)] and Mih concentrations are lower in males experiencing higher-than-normal temperature in various fish species (Elisio *et al*., 2012; Hermelink *et al*., 2013; Soria *et al*., 2008; Vikingstad *et al*., 2016), which may be caused by the inhibition of gonadotropin and the reduced expression of *lhβ* and *fshβ* described above. Similar results have been published on *C. gobio* males subjected to moderate or high temperature (+4°C or +8°C) in which plasma levels of 11-KT (for both temperatures) and T (+8°C only) were lower than in control fish (Dorts *et al*., 2012). This androgen depletion could be the cause of lower or decreasing GSIs mentioned above. The same tendency has been observed in *A. polyacanthus*, where levels of gonad steroid 11-KT did not increase as expected prior to spawning in warm

conditions, which likely arrested reproductive function (Donelson *et al*., 2010). However, the negative impacts of high temperature on 11-KT were mitigated by better nutritional status in this species (Donelson *et al*., 2010). Collectively, these studies indicate that male reproductive development and function are affected by high water temperature, with severe consequences above critical thermal limits, and such impacts appear to be underpinned by altered physiology across the BPG axis (Table 5). However, more studies on the earlier stages of spermatogenesis are necessary to gain a more wholistic understanding of temperature effects.

7 | OTHER FACTORS INFLUENCING THE SEVERITY OF TEMPERATURE IMPACTS

Several factors have been described which modulate the severity of temperature impacts such as pollution (Hani *et al*., 2019), nutritional status (Donelson *et al*., 2010; for review, see Pankhurst & Munday, 2011), age at spawning (Pankhurst *et al*., 2011) and transgenerational acclimation (Donelson *et al*., 2018). In this section, we touch on two areas with significant relevance to ecology, fisheries and aquaculture, age at spawning and transgenerational acclimation.

7.1 | Age at spawning

In females, age at sexual maturation can significantly influence reproductive investment and egg quality. In silver seabream [*Chrysophrys auratus* (Forster 1801)], 2-year-old maiden spawners had smaller relative gonad size than 3-year-old repeat spawners (Cleary *et al*., 2000). Similarly, the ovaries of maiden striped bass [*Morone saxatilis* (Walbaum 1792)] contained an abnormally heterogeneous population of oocytes that were comparatively smaller than the oocytes of repeat spawning fish (Holland *et al*., 2000). Further to this, maiden *M. saxatilis* produced eggs that contained a few (if any) yolk granules, which was markedly different to what was observed for repeat spawning individuals that had entered vitellogenesis (Holland *et al*., 2000). For other species such as *G. morhua*, *G. chalcogrammus* and *S. salar*, younger first-time spawning fish produce smaller eggs and have lower fecundity relative to repeat spawning fish (Kjesbu *et al*., 1996; Pankhurst *et al*., 2011; Solemdal, 1997; Tanaka *et al*., 2019; Trippel, 1998). Similarly, in the Gilthead seabream (*Sparus aurata* L.) younger fish produced smaller eggs but, in contrast to expectations, had higher fertilization rates and relative fecundity than older fish (Jerez *et al*., 2012). Age-dependent changes in egg quality appear to result in a loss of reproductive capacity, which has been measured as a reduction in the number of larvae produced by *G. morhua* per "maternal gram" (Trippel, 1998) or as a decrease in post-fertilization viability and hatchability in Murray cod [*Maccullochella peelii* (Mitchell 1838)] (Newman *et al*., 2008), for example.

Age-specific differences in reproductive physiology that likely contribute to changes in gamete quality have been described to some extent in several species. For example, the term "dummy run" has been used to describe a situation where the endocrine system is only partially activated in younger fish, and as a result viable gametes are not produced (Holland *et al*., 2000; Zmora *et al*., 2014). In *M. saxatilis*, sexual maturation for the first time (pubertal development) in 3-year olds was associated with a 34-fold increase in *fshβ* from basal levels compared to a 218-fold increase in 4-year olds (Hassin *et al*., 1999). Similarly, in *O. mykiss* circulating levels of Fsh were significantly higher in repeat spawning fish than in maidens (Prat *et al*., 1996), though it appears that the impact of age on endocrine function is not entirely consistent between species (see below). At the level of the ovary, E2 levels were lower during pubertal development compared to the second reproductive season in *M. saxatilis*, and it was hypothesized that this could be caused by reduced Fsh synthesis, and could have been responsible for the lack of yolk granules in oocytes from maidens (Holland *et al*., 2000). In contrast, plasma Fsh, E2 and Vtg, and hepatic *vtg*, and *zpb* levels were lower during early secondary oocyte growth in repeat spawning *S. salar* relative to maiden spawners, and despite this post-ovulation egg diameter/volume was significantly higher in repeats (Pankhurst *et al*., 2011). As maiden *S. salar* in those studies did not appear to undergo a dummy run, the differences in physiology may reflect the time needed for repeat spawning fish to "catch up" following the previous years' spawning event.

In addition to oocyte morphology and physiological characteristics, other egg quality parameters and spawning dynamics in different environmental conditions may be influenced by age. This has been demonstrated for captive individuals of *S. salar* where exposure to higher-than-optimal temperatures caused a significant reduction in egg fertility and eyed egg survival in maiden but not for repeat spawning fish (Pankhurst *et al*., 2011). At 22°C (simulated warm summer), spawning was also delayed to a larger extent in first-time spawning fish relative to older fish (Pankhurst *et al*., 2011). A similar phenomenon has also been observed in both captive and wild *G. morhua* where larger (older) females tended to spawn earlier than smaller (younger) females at warmer, but not colder temperatures (Kjesbu *et al*., 2010). The same tendency has been observed in *G. chalcogrammus*, as older fish tend to spawn earlier and for a longer time relative to young individuals in warmer conditions, but the phenological responses are nonlinear (Rogers & Dougherty, 2019).

From the few studies investigating male age and reproductive success, similar observations as for females have been reported. In *C. harengus*, first-time spawners were smaller and had lower GSI than repeat spawners (Evans & Geffen, 1998). Nevertheless, among the other parameters examined (*e.g*., sperm motility, ATP content, fertilization rate), none were influenced by age. In *M. saxatilis*, males had lower GSI and circulating levels of T and 11-KT during earlier reproductive cycles, and multiple reproductive cycles were required to achieve full reproductive capacity (Holland *et al*., 2000). However, very few studies have investigated this process, and more investigation is needed to elucidate the relationship between age and temperature at spawning in the context of reproductive physiology and success. Thus, demographic structure, especially for females, has the potential to influence the reproductive capacity of a population and this impact will be modulated by climate. Such complex interactions

might have implications for stock productivity and management (Kjesbu *et al*., 2010; Marteinsdottir & Thorarinsson, 1998; Scott *et al*., 1999).

7.2 | Transgenerational conditioning/acclimation

Climate change corresponds to a prolonged and overarching, but also possibly a rapid, evolution of environmental conditions and therefore will occur over several generations for most species (Donelson *et al*., 2016). Thereby, investigations are required to understand the multigenerational impacts and adaptation capacity of each species in a changing climate (*e.g*., phenotypic plasticity; Munday *et al*., 2013), which will elucidate the nongenetic inheritance mechanisms or epigenetic processes which enable transgenerational plasticity (TGP) (Donelson *et al*., 2012, 2018; Ryu *et al*., 2018). In recent years, TGP has received more interest as demonstrated by the increasing number of TGP studies in numerous taxa, including fish, and here we briefly cover some aspects relating to reproduction (for review see Donelson *et al*., 2018; Byrne *et al*., 2020).

Although TGP has been studied from one generation to the next (Shama *et al*., 2014; Thorn *et al*., 2019) or after several generations in teleosts (Donelson *et al*., 2012, 2016; Fuxjäger *et al*., 2019; Loisel *et al*., 2019; Ryu *et al*., 2020; Veilleux *et al*., 2018), few studies have investigated reproductive function and success. In the following sections, studies on *G. aculeatus* and *A. polyacanthus* will be discussed, as significant progress on understanding TGP in the context of reproductive function has been made for these species. First, in *G. aculeatus*, the experimental design consisted of the acclimation of the F0 adults at 17°C or 21°C to produce F1 crosses between the temperatures (Shama & Wegner, 2014). F1 offspring originating from these crosses were reared at one of two temperatures [17°C or 21°C, developmental temperature (DT)] from fertilization to the adult stage, and were then crossed within and between temperatures to produce an F2 generation. In addition, same temperature crosses were done in each generation. F1 egg size was not impacted by F0 acclimation temperature, but F2 egg size was mainly determined by maternal DT (Shama & Wegner, 2014). Indeed, females exposed to higher-than-optimal temperature during their entire life produced a higher numbers of smaller eggs than those in control conditions (Shama, 2015; Shama & Wegner, 2014). Moreover, F2 eggs from 21°C fish had lower hatching success. In another two-generation experiment on *G. aculeatus*, elevated maternal DT (21°C) caused a reduction in F2 (but not F1) egg size, without affecting the hatching success (Fuxjäger *et al*., 2019). However, a decrease in egg size was also observed when optimal DT (17°C) females were placed at 21°C during reproduction only, demonstrating the importance of temperature during reproduction, maternal DT, and the interaction between them over generations (Fuxjäger *et al*., 2019). In addition, mating success (*i.e*., number of realized matings divided by the number of all potential matings) was positively affected by TGP (Fuxjäger *et al*., 2019).

In the second species, *A. polyacanthus*, a similar experimental approach was used: a 1.5°C increase in two successive generations (stepwise increase, SWI) or a 3°C increase in the F1, followed by maintenance at the same temperature in the F2 (single transgenerational increase, STGI) (Donelson *et al*., 2010, 2016; Ryu *et al*., 2018, 2020; Veilleux *et al*., 2018). Under SWI across generations, some reproductive traits were positively (*e.g*., breeding proportion and egg number) or negatively (*e.g*., clutch size) impacted (Donelson *et al*., 2016). These impacts appear to be mediated by changes in gene expression, for example *fshβ*, *lhr*, *fshr* (Veilleux *et al*., 2018). Although the STGI regime resulted in negative transgenerational response (inhibition of reproduction), reproductive inhibition was reversible and reproductive function was partially restored once individuals were maintained at a lower temperature (Donelson *et al*., 2016). This result is important as it demonstrates that thermal impairment is not necessarily permanent, as found in other experiments (Elisio *et al*., 2012). In addition, SWI impacted phenology by advancing the spawning season of breeding pairs (Donelson *et al*., 2016) which was not detected in a within-generation exposure study in the same species and thermal conditions (Donelson *et al*., 2010).

Different species-specific mechanisms may be involved in determining TGP depending on the duration, timing and magnitude of exposure, rate of warming and number of generations. For example, TGP may be mediated by modifications of the epigenome, including DNA methylation (for review, see Labbé *et al*., 2017). Moreover, under optimal conditions, the epigenome is reprogramed during gametogenesis and early embryo development (Labbé *et al*., 2017). Since embryos are particularly sensitive to temperature, as are germ cells, temperature-induced epigenetic change during this stage/in these cells could have large implications for developmental plasticity (Donelson *et al*., 2018). Using the same protocol described above for *A. polyacanthus*, a recent study found that DNA methylation changed following exposure to high temperature, though less change was observed in SWI than in STGI relative to control fish (Ryu *et al*., 2018). Impacted genes included those associated with energy homeostasis, hypoxia, mitochondrial activities and vascular functions (Ryu *et al*., 2018). However, SWI fish did not present a significant difference in DNA methylation to improve reproductive capacity (*e.g*., breeding proportion) compared to STGI fish (Ryu *et al*., 2018). Nonetheless, very few studies have investigated the impacts of temperature on the epigenome across generations, as highlighted by Labbé *et al*., 2017.

Until recently, only a few species had been studied and, as raised by Donelson *et al*. (2016), more species-specific work is needed on TGP, especially in species with ecological or fisheries importance, to better understand the biological mechanisms involved under climate change. In addition, TGP can be mediated by either paternal or maternal mechanisms at elevated temperature (Shama *et al*., 2014; for review, see Donelson *et al*., 2018; Veilleux *et al*., 2018; Fuxjäger *et al*., 2019), highlighting the importance of studying both sexes in the context of global warming. Finally, Donelson *et al*. (2016) demonstrated that amplitude and rate of thermal change are important, as rapid warming may limit the ability of fish to adapt over several generations. Thus, some teleost species may be able to adapt to global

warming if temperature increases are gradual due to enhanced plasticity (Donelson *et al*., 2016).

8 | CONCLUSIONS AND FUTURE CHALLENGES

Successful recruitment is partly dependent on gamete quality contributing to developmental success in the next generation. Consequently, egg and sperm quality and fecundity are crucial for both aquaculture and fisheries, today and in the future. However, climate-driven warming will, or is already, negatively impacting teleost reproductive capacity, leading to reduced gamete quality and reproductive failure in some species. Therefore, it is paramount to understand the complex physiological mechanisms underpinning these impacts that likely occur at all, or a combination of levels on the BPG axis. Additionally, interaction with timing of thermal exposure or age at spawning, among others, can modulate those effects.

Although female reproductive cycle and performance have been intensively investigated, some gaps in knowledge remain. For example, the mechanisms involved in fecundity regulation, down-regulation by atresia and *de novo* recruitment of oocytes in the context of global warming leads to contradictory results depending on the species. In addition, a topic of great importance is the impact of global warming on teleost reproductive investment, and future approaches in this field should include emerging egg quality indicators from "-omics" approaches. Despite the increasing number of -omics studies, very few comprehensive investigations have been done up to now. Characterizing egg content (*e.g*., mRNAs) at higher-than-normal temperatures could help to elucidate upstream regulatory mechanisms and downstream changes in offspring fitness. Such findings can be complemented by data from multiple sampling points throughout the reproductive cycle, which will also help to link egg quality (including content) at spawning with physiological/developmental processes during gametogenesis. In doing so, the complex physiological mechanisms that contribute to the impacts of elevated temperature, for example Cyp19a1a enzyme activity or *foxl2* gene expression, will be more deeply investigated across taxa.

The impact of elevated temperature on gametogenesis, gamete quality and reproductive physiology has received far less attention in males than in females. Hence, an intensified research effort on thermal disruption of spermatogenesis, sperm quality and the physiological mechanisms involved, in addition to downstream impacts on the progeny, is needed to improve projections of climate impacts on teleost reproductive biology. In general, for both females and males, the early stages of gametogenesis should be incorporated into future temperature-impact studies as research on these phases is lacking. Finally, while current works mainly focuses on temperate species, for example salmonids, deeper investigations from a broader range of environments, from polar to tropical latitudes, could help to clarify the general mechanistic principles essential for our comprehension of how teleosts will respond to future environmental change. Future research aiming at deciphering impacts of climate change on teleost reproduction at multiple levels of biological organization depends on the contribution of emerging transgenerational acclimation and epigenetic studies. The scope of these future works should include field and laboratory experiments with a focus on physiology (*in vitro* and *in vivo*) and the integration of temperature data with other stressors, behavioural study on species and interactions with their prey (match–mismatch) coupled with advanced modelling. Together with advances in deciphering parental conditioning and heritability of resilience under global warming, this information will help us to better understand and project climate change impacts on wild populations, fisheries and aquaculture.

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ORCID

Maud Alix https://orcid.org/0000-0002-2365-9188
Olav S. Kjesbu https://orcid.org/0000-0002-8651-6838
Kelli C. Anderson https://orcid.org/0000-0001-7749-4641

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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